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SOME NORTH AMERICAN PARASITES OF BLOWFLIES[1]

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INTRODUCTION

Many are the interrelations between the insects involved in the decay and disintegration of animal carcasses. When an animal dies, if weather conditions are favorable blowflies are attracted immediately, and they deposit their eggs or young larvae, usually in the natural orifices. Ants may begin at once to carry away the newly deposited fly eggs, and later they will attack the larvae in the carcass. After fly larvae are present, beetles appear, and their numbers increase steadily. Some species of these beetles deposit eggs from which develop larvae that feed upon hide, hoofs, and horns; other species produce larvae that prey upon blowfly maggots, and some feed upon both carcass and maggots. The adults of nearly all the species of beetles that frequent carrion feed upon immature stages of flies, some occasionally, others almost exclusively.

There are, in addition, species of Hymenoptera that fly to the carcass and parasitize the blowfly larvae, the young parasite developing within the maggot until finally the fly larva, which in the meantime has transformed into a pupa, is completely consumed. When a parasitized maggot is attacked by a beetle or a beetle larva, both parasite and fly larvae are destroyed. After the carrion is consumed and the blowfly larvae have reached maturity, most of them migrate from the carcass and pupate in the soil in some favorable place a few feet or yards away. Many of these migrating maggots carry within them the developing young of their parasites, and even as they migrate they are further attacked by parasites and predators. Those maggots that remain and pupate unprotected within the carcass are often victims of Hymenoptera which parasitize dipterous pupae.

Other less important predators attack the blowflies in the adult stage. These predators usually prey on other insects as well as on flies.

FACTORS AFFECTING THE INSECTS

Many factors which are at work during these processes affect the blowflies and associated insects. The carcass may be consumed entirely or in part by various mammals or vultures, or it may be buried or burned. Total destruction of course ends the fly problem immediately, while partial destruction proportionately reduces the

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[2] The investigations of parasites and predators of blowflies were carried out at Uvalde, Tex. The data concerning the distribution of *Alysia* and *Psilodora* in California and Arizona were taken from records made by D. C. Parman. Distribution notes were also made on Arizona and New Mexico species by A. W. Lindquist. The author is indebted to the following specialists for the determination of specimens: Hymenoptera, A. B. Gahan, C. F. W. Muesebeck, L. H. Weld; Diptera, *Sarcophaga*, David G. Hall. The drawings were made by Miss Claudelle Lewis.

number of flies involved. Birds or other animals may also pick out all or a portion of the insects.

Climatic conditions act from the very beginning to influence the insect complex at the carcass. An animal dying in warm weather may be covered with fly blows before death, whereas at lower temperatures oviposition may be retarded for several hours or even for an indefinite period. Conditions that permit one species to oviposit may deter another. Very dry weather, particularly hot, dry winds, will lower the percentage of eggs that hatch. In southern Texas, during the summer months, sun scald is an important factor in causing the death of larvae in exposed carcasses.

The species of Diptera that develop in a carcass vary with the locality, season, size of carcass, and many other factors. Temperatures within the carcass influence differently the oviposition of various species. Often one species of fly, usually the dominant one of the season, is present in large carcasses almost to the exclusion of other flies, while in smaller carcasses a different species may be predominant. Competition occurs between the larvae of blowfly species, particularly in small carcasses; however, the results of some environmental or other factors should not be misconstrued as competition between species. There is a sequence in the infestation of a carcass by the different species of flies, but this is extremely variable. The observations of a distinct sequence frequently mentioned in literature have probably been based, to some extent, on the marked differences in time of emergence of the various species from pupae formed in the same carcass.

Physiological, bacteriological, and chemical conditions develop within the carrion which may hasten or retard the development of one or many species of insects.

Eggs, larvae, and pupae of the flies may be attacked by parasites or predators which may destroy them immediately or ultimately. A predator that destroys a fly larva early in the destruction of a carcass may merely make room for the development of another larva, and if a parasite has oviposited in a maggot that is later destroyed by a predator, the egg is wasted.

Despite the combined action of all these influences, some blowfly larvae mature and migrate. The number, however, is variable, and some factor or combination of factors may decrease the number of maggots maturing or the number of one particular species.

The writer believes that the most important influences on the development of blowflies in large carcasses, in the order of their importance, are: The destruction of the carrion by man or animals, environmental and physiological conditions, the destruction of maggots by parasites and predators, and the competition between the species of Diptera. In the case of small carcasses all these factors are operative, with the insect predators and parasites more effective than in large carcasses.

EXPERIMENTAL METHODS

In making tests with blowfly parasites, particularly with those brought to Uvalde from other localities, it was necessary to keep the insects in close confinement. As none of these imported para-

sites were released, field observations could not be made upon them under Uvalde conditions. In studying developmental periods and host preferences, parasites were placed in pint mason jars on meat infested with blowfly larvae. The jars contained 2 inches of sand in which the larvae could pupate, and were capped with 60-mesh brass strainer cloth. All experiments were conducted in a flyproof insectary to prevent infestation of the meat by other species of flies. Unless otherwise stated, the parasites were confined with the fly larvae, and it should be kept in mind that such experiments, particularly the host tests, were made under laboratory conditions.

For the status tests for blowfly parasites and predators, 4-ounce meat baits in pint mason jars were exposed in the field. Upon pupation of the infested larvae, the jars were capped and brought to the insectary.

A distinction is made in this paper as to size of carcasses. Large carcasses, such as those of cattle, horses, and even goats, are seldom, so far as known, frequented by parasites of blowflies, but around them are thousands of predatory beetles and ants that continually deplete the number of fly larvae. Small carcasses, such as those of rabbits, turtles, and armadillos, are frequented by many parasites and predators. The very small carcasses such as birds and fishes produce the largest percentage of infestation by fly parasites.

SOME INSECTS THAT FEED ON BLOWFLIES

There is given here a list of the insects that have been observed at the Uvalde laboratory to prey on blowflies, though not all of them are of great economic importance in relation to the blowflies.

HYMENOPTERA

Larval parasites	Pupal parasites
Braconidae	Braconidae
Alysia ridibunda Say	*Aphaereta muscae* Ashm.
Alysia fossulata (Prov.)	Diapriidae
Cynipidae	*Trichopria hirticollis* Ashm.
Psilodora sp.	Pteromalidae
Xyalosema armata (Say)	*Mormoniella vitripennis* (Walk.)
Xyalosema sp.	
Chalcididae	
Brachymeria fonscolombei (Dufour)	
Eniaca texana Ashm.	

ALYSIA RIDIBUNDA SAY

The parasite described by Say (*11, p. 380*)[3] in 1828 as *Alysia ridibunda* (fig. 1) belongs in the family Braconidae and subfamily Alysiinae. There is considerable difference in the sizes of the adults, as they range from 5 to 9 mm in length. The body is yellowish red, head black, the wings blackish brown, and the legs blackish. The ovipositor is exserted.

DISTRIBUTION

As indicated by specimens in the United States National Museum *Alysia ridibunda* is rather widely distributed, specimens being la-

[3] Reference is made by number (italic) to Literature Cited, p. 494.

beled as from New York, Maryland, Virginia, North Carolina, Florida, Michigan, Indiana, Illinois, Kansas, Texas, New Mexico, and Arizona. The insect has not been found at Uvalde, Tex., but a heavily populated area was found in Arizona (Pima, Pinal, Cochise, Santa Cruz, Graham, and Greenlee Counties) and another in New Mexico (Socorro, Luna, and Dona Ana Counties). From 1930 to 1933 this parasite was not collected elsewhere in Arizona or New Mexico. During the same period it was not found in collections from Texas, California, Arkansas, Kansas, Louisiana, Mississippi, Georgia, North Carolina, or Florida, although an extensive search was made.

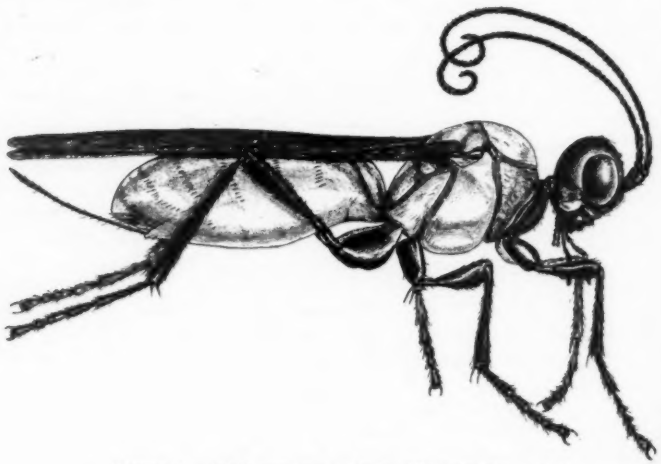

FIGURE 1.—Adult female of *Alysia ridibunda* Say. × 8.

HABITS

The habits of *Alysia ridibunda* have been studied only under laboratory environment. The insect breeds readily in confinement, if tended properly, and, generally speaking, develops uniformly by broods. The progeny obtained from material collected in 1931 parasitized fly larvae and developed an overwintering generation which, upon emergence in the spring of 1932, produced another generation.

Adults of this species kept in confinement at an average daily mean temperature of 85° F. and furnished with such foods as honey, meat, and fruit lived from 3 to 7 days. It is probable that the life of the adults could be lengthened considerably by keeping them under more natural conditions and at lower temperatures.

The females mate as early as the day of their emergence, and they may be placed either upon meat containing various stages of blowfly larvae or directly upon mature larvae that have migrated after feeding. The long ovipositor is thrust into any portion of the body of the fly maggot. Ordinarily only one egg is deposited at a single insertion of the ovipositor. Usually the parasite stands directly above the larva, the tip of the ovipositor being forced downward and at the same time forward between the parasite's legs.

Developmental Period

Eggs of *Alysia ridibunda* hatch in 24 hours at 80° F. Frequently under conditions of confinement as many as 10 parasite eggs may be placed in one host larva. On the second day following hatching there is a marked variation in size of the parasites within each individual host. Nearly always one parasite develops much faster than the others. At the end of 7 days, ordinarily only one parasite remains alive in each host, though in a few instances two have been found. In no case, however, did more than one parasite complete development in a host. The supernumerary parasites die in the first instar. At 80° pupation takes place about the twentieth day, and the adults emerge about 7 days later. The parasitized host larva forms its puparium at the conclusion of the feeding period, after which the parasite completes its development. The latter then pupates within the puparium and lies with its head directed toward the anterior end of the puparium. The adult parasite later emerges by cutting through this end of the puparium.

During 1931 and 1932 about 300 specimens of *Alysia ridibunda* were reared in the laboratory insectary. The earliest emergence from overwintering specimens was on March 19. The last oviposition occurred November 22. All material obtained during November overwintered as larvae or pupae in host pupae of *Calliphora coloradensis* Hough, *Sarcophaga plinthopyga* Wied., or *S. misera* var. *sarracenioides* Ald. In January and early February, at Uvalde, *A. ridibunda* was found hibernating as mature larvae or prepupae. By February 25 they had transformed to the pupal stage.

In the summer broods the shortest developmental period, from egg to adult, was 20 days, the longest 45 days. The average developmental period at an average daily mean of 76° to 80° F. was 27 days, but the average period increased to 45 days when the temperature was 66° to 70°. The overwintering individuals required an average of 151 days for development, with extremes of 121 and 174 days.

Hosts

Alysia ridibunda was reared in the laboratory from the following species of flies: *Sarcophaga plinthopyga*, *S. misera* var. *sarracenioides*, *Lucilia sericata* Meig., *L. unicolor* Towns., *Calliphora coloradensis* Hough, and *Synthesiomyia nudiseta* v. d. W. Attempts to rear the parasite in *Ophyra leucostoma* Wied. and *Cochliomyia macellaria* Fab. were unsuccessful. Twenty-four tests were conducted to determine from which species of flies the parasite could be reared. These tests were conducted as follows: In each test the progeny of a single female fly or the combined progenies of several females of the same species were placed on meat, and while feeding were exposed in a cage containing several mated pairs of *A. ridibunda*. After the fly larvae had matured they were allowed to pupate in sand and from these the emergence of blowflies and parasites was recorded. The results of the tests of hosts of *A. ridibunda* are given in table 1.

TABLE 1.—*Emergence of Alaska ridibunda from blowfly hosts at Uvalde, Tex., 1931–32*

Host	Total tests	Successful tests	Average adult parasites per test	Emergence			
				Total	Blowflies	Parasites	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Percent*
Sarcophaga	14	7	31	346	131	215	62
Calliphora coloradensis	1	1	37	91	54	37	41
Lucilia sericata	2	2	8	81	66	15	19
Lucilia unicolor	2	1	1	25	24	1	4
Synthesiomyia nudiseta	1	1	1	224	223	1	.4
Cochliomyia macellaria	3						
Ophyra leucostoma	1						
Total or average	24	12	22	767	498	269	35

Alysia ridibunda strongly resembles *Brachymeria fonscolombei* in its host preferences, being distinctly partial to *Sarcophaga*, breeding readily in *Calliphora*, to a less extent in *Lucilia*, and very rarely in *Cochliomyia*.

ALYSIA FOSSULATA (PROV.)

Provancher (*9, p. 391*) based his description of *Alysia fossulata* on a specimen from Los Angeles, Calif. The adult is about 5 mm in length, with the head, thorax, and abdomen black and the legs brown. The wings are transparent but with a slightly brownish cast. The ovipositor does not extend beyond the apex of the abdomen.

DISTRIBUTION

Specimens in the United States National Museum, together with Provancher's record and the writer's recent status work, indicate that the species is present in the low valleys of the coastal area of California. This area extends from Alameda and Santa Clara Counties through Monterey County. In the Salinas Valley of Monterey County the parasite was abundant during 1932. Specimens were collected also in Los Angeles County.

DEVELOPMENTAL PERIOD

At Uvalde, Tex., adults of *Alysia fossulata* reared in the laboratory from material collected in Salinas, Calif., were very active and readily attacked blowfly maggots. Fly larvae were parasitized from November 6 to December 1, 1932, and another generation of 33 parasites was obtained. They did not appear to hibernate during cold weather, for they emerged between January 16 and February 18, 1933. The average developmental period was 80 days with extremes of 71 to 101 days. One lot was reared from *Sarcophaga plinthopyga*, one lot from *Lucilia* sp., and two lots from mixed species of blowflies. Adults of the second-generation parasites lived from 5 to 17 days, unprotected, through a minimum temperature of 14° F. The females attacked blowfly maggots, and oviposition apparently occurred, but no progeny survived.

PSILODORA SP. (? *Psilodora rufocincta* Kieffer)

The genus *Psilodora* belongs in the family Cynipidae, subfamily Eucoilinae. In the Uvalde laboratory collection there are specimens of the species studied that range in length from 2.5 to 5 mm. The color of the head and body appears to be black but upon closer examination is found to have a brownish cast; the legs are reddish brown; the antennae are dark brown, those of the female 13-jointed

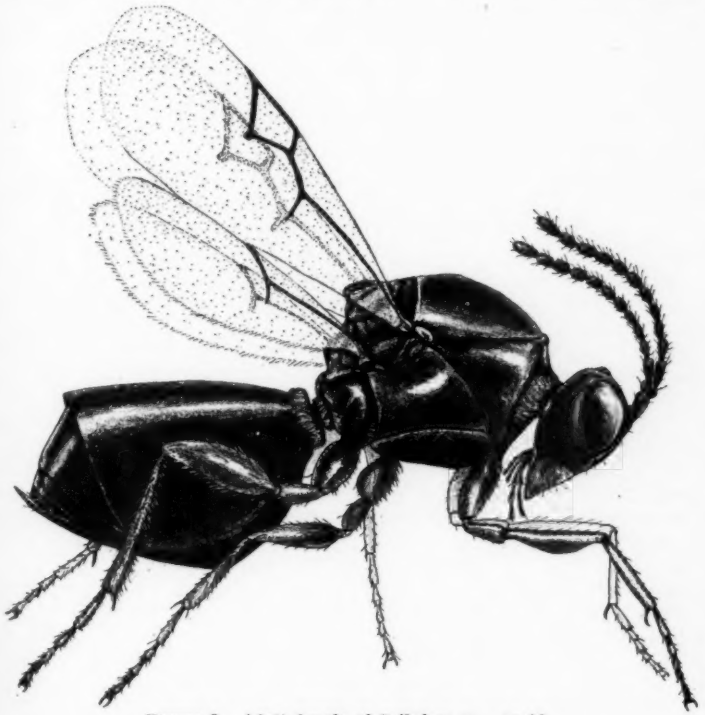

FIGURE 2.—Adult female of *Psilodora* sp. × 16.

(fig. 2), subfiliform, pubescent, those of the male 15-jointed, filiform, lightly pubescent; the scutel has a cuplike elevation above; the abdomen has a hairy girdle at the base.

DISTRIBUTION

This species is confined to the western part of the United States. It was found most abundant throughout Arizona and New Mexico, and to a lesser extent in California (Riverside, Imperial, Kern, Monterey, San Benito, and Santa Clara Counties), Kansas (Pratt and Sedgwick Counties), and Texas (Dallas, Uvalde, and the Panhandle counties). L. H. Weld has observed and collected this species at Oregon Caves, Oreg. This is the most northern record; Dallas, Tex., the most eastern, and Uvalde, Tex., the most southern, in the writer's notes.

Habits

Psilodora sp. has been recorded frequently as a parasite of maggots breeding in cow dung. The adult of this species has been observed to enter the fresh dung and seek out the maggots, returning to the outside when its work was finished. There is no doubt, however, that under natural conditions this species also infests carrion-breeding maggots, as it has been reared hundreds of times from blowfly larvae in field exposures. The female parasite attacks the larva of the fly, piercing the body wall at any point with her ovipositor and placing one or more eggs in the coelomic cavity. Although all these eggs may hatch, only one parasite completes development. Numerous parasitized pupae have been put in individual glass vials, but not more than one parasite has ever emerged from a single host.

The adults will mate as early as the day of emergence, and about 20 seconds may be consumed in the process of mating. The male will continue to court the female, but is repulsed repeatedly. The female begins oviposition the day of emergence if host larvae are available.

Parthenogenetic reproduction was demonstrated in three tests in which unmated females that emerged in individual glass vials were placed in jars containing blowfly larvae. These larvae, when reared, produced a total of 23 *Psilodora*, sp., all males. The average development period of 35 days was normal for the parasite.

Adults of *Psilodora* sp. in confinement at an average daily mean temperature of 82° F. (extremes 63° to 99°), when given no food or water, lived for an average of 5 days with an extreme of 10 days. When furnished with such food as bananas, figs, or honey, the average longevity was extended to 8 days with an extreme of 18 days. The adult life is probably longer under natural conditions and at lower temperatures.

Developmental Period

In laboratory tests in 1931 and 1932, 799 *Psilodora* sp. were reared. It is evident from data obtained that this species has a longer developmental period than *Alysia ridibunda* or *Brachymeria fonscolombei*. The overwintering individuals go into hibernation at higher temperatures and remain thus for a longer period; and in the summer broods the developmental period was extremely variable. There is a tendency for some individuals to remain for long periods in the pupal stage. An example of these variabilities is shown by a group of larvae parasitized late in August 1931; from these a number of *Psilodora* emerged, beginning the twenty-eighth day and continuing to the eighty-first day; the remainder of the brood overwintered, some not emerging until 225 days after oviposition. However, in spite of this, *Psilodora* is easily handled and is well adapted for rearing by artificial means.

The earliest emergence of *Psilodora* was recorded for March 2, and the latest oviposition November 22. The records include only broods resulting from ovipositions between March 31 and September 18. The extremes of the developmental periods of the summer broods were 27 and 81 days; and for the overwintering parasites, 112 and 225 days. The average developmental period from egg to adult at

an average daily mean temperature of 71° to 75° F., was 50 days; at from 76° to 80°, 43 days; and from 81° to 85°, 34 days. Overwintering material kept at an average daily mean temperature of from 61° to 65° (minimum, 21°) required an average of 195 days for development.

Psilodora sp. hibernated in 1932 during December, January, and part of February as mature larvae or prepupae in the host puparia. By February 25 the parasite pupae were well developed. Hosts for overwintering *Psilodora* were *Synthesiomyia nudiseta*, *Sarcophaga plinthopyga*, and *Cochliomyia macellaria*.

Hosts

Thirty lots of blowflies were exposed to *Psilodora* sp. under laboratory conditions and parasites were reared from the following: *Sarcophaga plinthopyga*, *S. misera* var. *sarracenioides*, *S. bullata* Park., *S. pedunculata* Hall, *Lucilia sericata*, *Cochliomyia macellaria*, *Synthesiomyia nudiseta*, and *Ophyra leucostoma*. The results of the tests of hosts for *Psilodora* sp. are given in table 2.

Table 2.—*Emergence of Psilodora sp. from blowfly hosts at Uvalde, Tex., 1931–32*

Host	Total tests	Successful tests	Average adult parasites per test	Emergence			
				Total	Blowflies	Parasites	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Percent*
Synthesiomyia nudiseta	2	2	75	210	59	151	72
Sarcophaga	11	5	21	155	50	105	67
Lucilia sericata	7	6	45	521	250	271	52
Cochliomyia macellaria	7	4	6	220	198	22	10
Ophyra leucostoma	3	1	1	75	74	1	1
Total or average	30	18	31	1,181	631	550	47

The greatest number of positive tests was made with *Lucilia sericata*, and 45 parasites per test were obtained, as compared with 21 parasites per test of *Sarcophaga* and 31 for an average of all tests. Apparently *Cochliomyia macellaria* is capable of acting as a host in spite of its short life cycle and the long developmental period of *Psilodora*. Four out of seven tests with this blowfly were successful.

XYALOSEMA ARMATA (SAY)

Xyalosema armata is a member of the family Cynipidae, subfamily Figitinae. The adult insect is 3.5 to 5.5 mm long. The body and head are black with a brownish cast; the antennae are brown except the first segment, which is black; the legs are reddish brown. The antennae in the female are 13-jointed, subfiliform; in the male, 14-jointed, filiform. The scutel ends in a spine.

Distribution

Xyalosema armata is of eastern and middle-western distribution. The writer's collection contains specimens from the following States: Kansas (Pratt, Kingman, Sedgwick, and Sumner Counties), Oklahoma (Grant, Garfield, and Stephens Counties), Texas (Delta

County), Louisiana (Webster Parish), Mississippi (Grenada County), Arkansas (Hempstead, Pulaski, St. Francis, and Crittenden Counties), Illinois (Knox, Henry, Mercer, and Warren Counties), and Florida (Orange County). It is listed among the Hymenoptera of Connecticut (*12*) and is found no doubt, over all the Eastern States. Its western limits are probably Pratt and the adjoining counties of central Kansas.

Habits

While this species breeds freely in blowfly larvae and was reared easily in jars containing meat baits in its natural habitat, it could not be reared satisfactorily in this manner at the Uvalde laboratory, although all the common species of blowflies were used. It is probable that the species is averse to breeding in the confinement of jars in the insectary, as trouble was experienced in attempts to rear other species of *Xyalosema*, but it is also possible that the parasite is not adapted to the climate of Uvalde.

Twenty-five host tests with both early instar and mature host larvae were made from May to November, but in two instances only were parasites obtained. *Xyalosema armata* was reared during August from *Sarcophaga bullata*, 27 parasites emerging after an average developmental period of 40 days; and from *S. plinthopyga*, 4 parasites emerging after an average developmental period of 47 days. The average daily mean temperature during these tests was 80° F. This developmental period of 40 to 47 days in *X. armata* is near that for *Psilodora* sp. at the same temperature.

Male and female adults of *Xyalosema armata* if placed together upon emergence will begin courtship immediately. The female will not accept the male a second time, but a male has been observed to mate with six different females within an hour.

The preoviposition period is very brief. A female that emerged one morning was mated at 10 and placed with blowfly larvae from 10:30 until 1 the same day. From these larvae were reared both males and females of *Xyalosema armata*. This demonstrates that fertilized eggs can be produced within 3 hours after the male and female are placed together and in the first half day after their emergence.

XYALOSEMA SP.

Another species of *Xyalosema* is very similar in appearance to *X. armata*, being about the same size and having about the same coloration.

Distribution

This species seems rather limited in its distribution. It is abundant along the coast of southern Texas, but has been found in only very small numbers elsewhere. Collections have been made in Texas (Cameron, Uvalde, Val Verde, Lubbock, Hale, and Swisher Counties), Oklahoma (Texas County), Colorado (Weld County), and Mississippi (Grenada County).

Habits

The parasite was first observed by the author in February 1929 at Brownsville, Tex. Two females were seen upon a 5-pound meat bait that had been exposed to attract blowflies. The parasites were run-

ning about over the meat and down into crevices searching for larvae. They were caught and placed in jars with blowfly larvae; these they parasitized and from them were reared a second generation. This parasite is probably active all winter at Brownsville, as are the blowflies. The parasites were found there again in April 1930, and several were placed upon *Sarcophaga* larvae. A second generation of *Xyalosema* was obtained at an approximate average daily mean temperature of 75° F. with an average developmental period of 55 days. During the same period a small number of males were reared from larvae of *S. plinthopyga* parasitized by unmated females, thus demonstrating parthenogenetic reproduction.

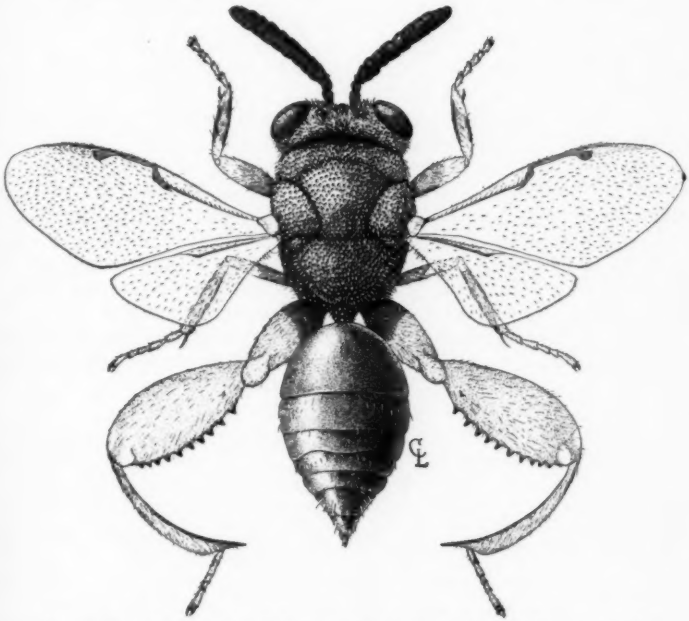

FIGURE 3.—Adult female of *Brachymeria fonscolombei* (Dufour). × 12.

From blowfly larvae taken in a meat bait exposed under field conditions at Uvalde from August 9 to 19, 1932, five *Xyalosema* sp. were reared with an average developmental period of 31 days. These specimens were placed in turn upon six unmixed lots of *Lucilia*, *Cochliomyia*, and *Sarcophaga* larvae, but another generation of parasites was not obtained.

BRACHYMERIA FONSCOLOMBEI (DUFOUR)

Brachymeria fonscolombei belongs to the superfamily Chalcidoidea, family Chalcididae. The adult insect (fig. 3) ranges from 3 to 6 mm in length; the head and body are black, the antennae black, and the legs red with yellowish-white markings; the posterior femur is enlarged, oval, and armed on the lower side with 10 teeth.

Distribution

The distribution of *Brachymeria fonscolombei* in the United States seems to be limited only in a northerly direction. Specimens in the writer's collection are from California, Arizona, New Mexico, Texas, Oklahoma, Kansas, Arkansas, Louisiana, Mississippi, Illinois, Maryland, and Florida. Galesburg, Ill., is the most northern record in the writer's notes.

Habits

The biology of *Brachymeria fonscolombei* has been discussed fully by the author elsewhere (*10*). This parasite attacks either mature or early instar larvae of blowflies, and not more than one adult emerges from each blowfly pupa. The preoviposition period is brief; females will mate the day of their emergence and produce fertile eggs. Without food or water, at 70° to 79° F., adults live about 4 days. Honey or fruits, when given as food, increase the average longevity to as much as 11 days.

Developmental Period

The developmental period from egg to adult averages 21 days at an average daily mean temperature of 86° to 90° F. At lower temperatures this period increases until at 65° the average developmental period is 35 days. As the temperature drops still lower a portion of the brood will overwinter as last instar larvae in the host pupae. The developmental period of *Brachymeria fonscolombei* is considerably shorter than that of *Psilodora* or *Xyalosema.*

Hosts

Brachymeria fonscolombei has been reared from the following species of field-collected and laboratory-reared blowflies: *Calliphora coloradensis*, *Lucilia sericata*, *L. unicolor*, *Phormia regina* Meig., *Cochliomyia macellaria*, *Sarcophaga plinthopyga*, *S. impar* Ald., *S. haemorrhoidalis* Fall., *S. carnaria* L., and *Synthesiomyia nudiseta.*

It is most active as a parasite of *Sarcophaga.* However, it readily parasitizes *Synthesiomyia* and *Phormia* and is frequently reared from *Lucilia* and *Calliphora.* The parasite was rarely reared from *Cochliomyia macellaria*, and it was demonstrated that ordinarily when *Brachymeria fonscolombei* parasitizes this fly both host and parasite larva die.

Brachymeria fonscolombei is found breeding in host larvae in carcasses of birds, rabbits, turtles, and other small animals. At Uvalde about one-third of the blowfly larvae in small carcasses are parasitized.

ENIACA TEXANA ASHM.

Eniaca texana, belonging to the family Chalcididae, subfamily Chalcidinae, has been reared in two instances from blowfly larvae.

On July 10, 1932, a 4-ounce meat bait was exposed in a small bush in a rather open location near Uvalde. The bait was brought in on July 20, and from the blowfly larvae infesting it were reared seven specimens of *Eniaca texana* after a developmental period of about

22 days. The host pupae, *Sarcophaga plinthopyga*, were confined separately in glass vials, and a single parasite was seen to emerge from each infested pupa. These parasites were placed with larvae of *Lucilia*, *Sarcophaga*, and other blowflies, but another generation was not obtained.

Blowfly larvae of various species were exposed at Encinal, Tex., April 5, 1933, and from these were reared five specimens of *Eniaca texana*. The developmental period of this lot was approximately 30 days.

APHAERETA MUSCAE ASHM.

Little is known of *Aphaereta muscae*, which belongs to the family Braconidae, subfamily Alysiinae, except that it emerges occasionally from baits containing blowfly pupae.

Viereck (*12, p. 214*) states that the insect "occurs" in Connecticut in July and August and that it has been reared from the onion maggot. Leonard (*7, p. 919*) lists it as common in New York and throughout the Eastern States. The author has reared it from blowfly pupae exposed by H. H. Stage at Salmon River Junction, Oreg., and has collected it over fresh cow dung at Victoria, Tamaulipas, Mexico. At Uvalde, Tex., it has been reared from a mixed lot of blowfly pupae, but in such large numbers (100 in a 4-ounce bait) as to suggest that it was breeding in *Sarcophaga* or *Lucilia*.

TRICHOPRIA HIRTICOLLIS ASHM.

Trichopria hirticollis is a parasite of blowfly pupae and belongs to the family Diapriidae, subfamily Diapriinae. It is encountered at Uvalde, Tex., each year from July to October. In one instance it emerged in April. From adult parasites collected in the field another generation can be reared easily in confinement.

No accurate data have been collected on the life history of this parasite, but it has been reared several times from *Sarcophaga plinthopyga* after a developmental period of 25 to 30 days. The average developmental period is probably shorter than this. As *Trichopria hirticollis* emerges at the same time as *Mormoniella vitripennis* from material exposed in the field, it is probable that their developmental periods are of about the same length.

From one lot of parasitized blowfly pupae of miscellaneous species, an average of 23 *Trichopria hirticollis* per host puparium was obtained. The maximum was 44 parasites from one puparium. In another test 32 parasites were secured from one puparium of *Sarcophaga plinthopyga*.

MORMONIELLA VITRIPENNIS (WALK.)

Mormoniella vitripennis (*Nasonia brevicornis* Ashm., *Pteromalus abnormis* Boh.) belongs to the family Pteromalidae. Girault and Sanders (*4*) in redescribing *M. vitripennis* give the following data concerning its size and color. Female: length, very variable, 1.0 to 2.30 mm, average 1.75 mm; color, metallic dark brassy green. Male: length, very variable, 0.60 to 2.0 mm, average 1.32 mm; color, lighter than female, more brassy, metallic, and green.

This small parasite of blowfly pupae is practically world-wide in its distribution. Gahan (*3*) states that in the United States it

occurs from New Jersey and North Carolina to California. It is probably the most important of the parasites attacking blowfly pupae, but even so it is of no great economic importance. The large numbers of this insect seen about carrion and the readiness with which it will attack pupae are misleading as to its value. Of 79,604 blowfly larvae reared from 1929 to 1932 at Uvalde, only 0.7 percent were parasitized by *Mormoniella vitripennis*. This is probably about its normal parasitization of blowflies. During the year of its maximum abundance since these studies have been under way, those reared amounted to only 1 percent of the total emergence of flies and parasites. As with other parasites of pupae it can act only on those flies which pupate in a fairly exposed place. At Uvalde, the chief value of this parasite is in its parasitization of the few pupae of fly larvae that fail to migrate and pupate within the carrion. One hundred percent of such pupae may be parasitized.

Various authors give the length of the life cycle as 11 to 27 days. At Uvalde, in the summer months, the parasite develops from egg to adult in an average of 14 days, the developmental period lengthening with cooler weather. *Mormoniella vitripennis* overwinters in the host puparium as mature larvae or as pupae, and overwintering specimens have required as long as 140 days for development. The species is inclined to continue breeding, however, whenever temperatures are favorable, and it is likely to begin emergence on any warm day during the winter. It has hibernated successfully in pupae of *Cochliomyia macellaria* as well as in other blowflies.

From observations at Uvalde, and from records of other workers, it appears that *Mormoniella vitripennis* will infest pupae of all the species of blowflies and of many other Diptera. At Uvalde it has been reared from *Cochliomyia macellaria*, *Phormia regina*, and numerous species of *Lucilia*, *Sarcophaga*, and *Calliphora*, both from field-collected and laboratory-reared hosts. The author has reared it from the cheese skipper, *Piophila casei* L.; Bishopp et al. (*1*) reared it, although not under field conditions, from *Hypoderma lineatum* De Vill.; Fujita (*2*) found it infesting *Tricholyga bombycis* Bech., a tachinid parasite of the silkworm; and Johnson (*6*), in discussing injury to nestling birds by *Protocalliphora*, refers to several instances of parasitization of *Protocalliphora* by *M. vitripennis*.

It is important to know the number of *Mormoniella vitripennis* which normally develop within each host puparium in order that when a given number of pupal parasites have emerged, the number of host pupae destroyed may be estimated. The number of parasites per fly puparium is dependent primarily on the host species. Hardy (*5*) states that 40 parasites may be reared from a single puparium, but that an average of 7 emerge from a single puparium of *Lucilia*. Fujita (*2*) obtained 37 parasites per puparium from the tachinid *Tricholyga bombycis*. At Uvalde, an average of 36 *Mormoniella vitripennis* was obtained from each puparium of *Sarcophaga plinthopyga*. An average of 46 (maximum 85) *Mormoniella vitripennis* were reared from a lot of 33 pupae of *Sarcophaga* spp., and an average of 36 parasites per puparium from *Phormia regina*.

ADDITIONAL NOTES ON PARASITES

There are a few other parasites that have been infrequently collected or of which the exact status is not known. In July 1930 numerous specimens of a species of *Xyalosema* were reared from *Cochliomyia macellaria* at San Luis Potosi, Mexico, by R. C. Mundell. In April 1931, however, extensive collections by the author at San Luis Potosi revealed none of these parasites, probably because it was too early in the year.

A specimen of *Eucoila* sp. was found on a meat bait containing blowfly larvae at Washington, D. C., in July 1932.

Pachycrepoideus dubius Ashm. is world-wide in distribution and is recorded from many parts of North America as a parasite on Sarcophagidae, Muscidae, dung flies, and other Diptera. Numerous specimens were reared by D. C. Parman at Ulvade in October 1928 from pupae in a meat bait.

In May 1930, 90 specimens of *Muscidifurax raptor* Gir. were reared from a lot of over 1,000 pupae of *Musca domestica* L. collected by F. C. Bishopp in April at El Paso, Tex. In the writer's collection are specimens of *M. raptor* reared in September 1914 by W. E. Dove at Dallas, Tex., from pupae of Diptera breeding in garbage.

Spalangia muscidarum Richardson is commonly reared from *Stomoxys calcitrans* L., as discussed by Pinkus (*8*). This species and others of the same genus appear frequently in breeding work with blowflies. The author has reared it in two instances while working with *Lucilia sericata*. In each instance, however, it emerged in very small numbers and might have been breeding in very small Diptera (*Aphiochaeta iroquoiana* Mall.) which were present in the meat.

SUMMARY

Blowflies breeding in carcasses are affected by the following factors: (1) Destruction of the carrion by man or animals, (2) environmental and physiological conditions, (3) destruction of maggots by parasites and predators, and (4) competition between the species of Diptera. Hymenopterous parasites are most active in small carcasses such as rabbits, turtles, and birds.

Species of the genera *Alysia*, *Psilodora*, *Xyalosema* and *Brachymeria* attack blowfly larvae. These species deposit their eggs within the bodies of fly maggots and produce but a single parasite in each host. *Brachymeria* and *Alysia* breed most readily in *Sarcophaga* but are reared also from *Calliphora*, *Lucilia*, and other blowflies. *Psilodora* and *Xyalosema* have a wider range in host selection and breed to some extent in *Cochliomyia*. *Alysia* and *Psilodora* were found in abundance in the Southwestern States, although occasional eastern and northern records are known. *Brachymeria* was found throughout the southern and central parts of the United States. *Xyalosema* is mainly of eastern distribution, although one species is found in the Texas coastal region. All of these parasites are of value because of the extent of their parasitism of blowfly larvae in carcasses. Especially important are those known to attack *Cochliomyia*.

Of the parasites which affect blowfly pupae, *Mormoniella* is the most important. *Aphaereta* and *Trichopria* are commonly encountered. These parasites produce a number of offspring in a single

host pupa and may easily be reared in large numbers under laboratory conditions. Their effectiveness in blowfly control is not great, however, because most fly larvae pupate in the soil where they are well protected from parasites.

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BRACHYMERIA INTERMEDIA (NEES), A PRIMARY PARASITE, AND B. COMPSILURAE (CWFD.), A SECONDARY PARASITE, OF THE GYPSY MOTH [1] [2]

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INTRODUCTION

Brachymeria intermedia (Nees) is a European species parasitic on the gypsy moth (*Porthetria dispar*. L.), as well as many other species of Lepidoptera. It was reared as early as 1905 from gypsy moth pupae sent to the Bureau of Entomology laboratory at Melrose Highlands, Mass. Since that time several unsuccessful attempts have been made to establish it in New England.

Brachymeria compsilurae (Cwfd.) is a parasite of tachinid flies which is apparently native to North America. It probably was of slight economic importance until after the establishment in New England of two European tachinids, *Compsilura concinnata* Meig. and *Sturmia scutellata* R. D., parasitic on the gypsy moth. Crawford (*6*)[3] first described it in 1911, and five of his paratypes were reared from *C. concinnata*. It is now recognized as an important enemy of both these beneficial insects.

Some observations on *Brachymeria compsilurae* were begun in 1924, but this work was interrupted in 1925 and also from 1928 to 1931, inclusive, while the writer was stationed in central Europe. The work in Europe consisted in collecting and shipping beneficial insects to the United States, and provided an opportunity for studying *B. intermedia*. It soon became apparent that, although there is a close morphological relationship between the adults of *B. intermedia* and *B. compsilurae*, there is a radical difference in the bionomics of the two species; furthermore, their immature stages exhibit marked differences. Because both of them may be important factors in the control of *Porthetria dispar*, it was decided to present the results of investigations on both species in a single paper.

LITERATURE ON BRACHYMERIA

Until recently the genus *Brachymeria* has been known as *Chalcis*, and nearly all references in the literature are under the genus *Chalcis*. It is a large genus, including more than 150 described species. Most of these species are found in tropical or subtropical climates, although many are common in the Temperate Zone, and some have a very wide distribution. *B. fonscolombei* (Dufour) is well distributed over Europe

[1] Received for publication Jan. 8, 1935; issued May 1935.

[2] This study was conducted at the Melrose Highlands, Mass., laboratory of the Bureau of Entomology during 1924, 1932, and 1933, and at its European sublaboratory, Budapest, Hungary, during 1929 and 1930. The writer is indebted to C. W. Collins, in charge of the Melrose Highlands laboratory, for making these investigations possible; to C. F. W. Muesebeck, D. L. Parker, and T. H. Jones for helpful advice and the use of notes which each of them made on these species; and to W. F. Sellers for help in collecting material in Europe.

[3] Reference is made by number (italic) to Literature Cited, p. 522.

and North America and has been found in Asia. *B. ovata* (Say) is common throughout the United States and the West Indies, and has recently been taken in Argentina. Many of the species are primary parasites of Lepidoptera. Pests of some of our most important crops, including cotton, sorghum, bananas, coconuts, and sugarcane, are heavily parasitized by members of this genus. A few species are definitely hyperparasitic, attacking tachinid parasites of Lepidoptera and sarcophagid parasites of Orthoptera; and one species, *B. secondaria* (Ruschka), has been noted as a secondary parasite of Hymenoptera. Several species attack sarcophagid flies which feed on carrion; and two species, *B. vitripennis* (Först.) and *B. euthyrrhini* (Dodd), are parasites of Coleoptera.

In spite of the size and importance of the genus, only one species, *Brachymeria fonscolombei*, has been studied in detail. As early as 1840 Dufour (*7*) described this species (under *Chalcis*) and gave an account of its life history. In 1923 Parker (*19*) gave further notes on its biology, and in 1924 he (*20*) fully described and illustrated the immature stages. In 1933 Roberts (*24*) published a paper on the biology of *B. fonscolombei* as a parasite of blowfly larvae.

Short accounts of several other species of *Brachymeria* have been published, however. *B. intermedia* was discussed briefly, under the name *Chalcis flavipes*, by Howard and Fiske (*11*) in 1911. A short resume was given of the parasite's life history, with figures of the full-grown larva, pupa, adult, and exit holes in *P. dispar* pupae. Burgess and Crossman (*1, p. 116*) also outlined its life history in 1929. They summarized rearings of *B. intermedia* from *P. dispar* pupae in Europe, and recorded the number of adults liberated in the United States; they also discussed the possibility of the establishment of the parasite in New England, and reviewed the host relations of the species. In 1924 Silvestri (*28, pp. 81–82*) published notes on this species as a parasite of *Tortrix viridana* L. In 1931 Martelli (*13, pp. 205–207*) gave a brief account of the biology of *B. intermedia* var. *scirropoda* (Först.), a parasite of *Aporia crataegi* L. In 1889 Stefani (*29*) published a short paper on (*Chalcis*) *Brachymeria dalmani* (Thoms.) as a parasite of sarcophagids. In 1929 Olsoufiev (*17, pp. 95–99*) discussed the same insect as a parasite of four species of sarcophagid flies parasitic on the Asiatic locust (*Locusta migratoria* L.) in Russia. He described the adult, the fifth-stage larva, and the pupa, and gave notes on its life history. Rukavishnikov (*25*) reported on the same species as a parasite of the same sarcophagids in 1930.

In 1897 Howard (*10*) published a short account of (*Chalcis*) *Brachymeria ovata* (Say) as a parasite of (*Orgyia*) *Hemerocampa leucostigma* S. and A., including figures of the adult, pupa, pupal exuvia, and exit hole in a parasitized pupa. Howard and Fiske (*11, p. 242*) in 1911, and Burgess and Crossman (*1, p. 118*) in 1929, gave brief resumes of the life history of (*Chalcis*) *Brachymeria obscurator* (Walk.). In 1923 Paillot (*18*) wrote a short paper on (*Chalcis*) *Brachymeria femorata* (Panz.), a parasite of *Pieris brassicae* L., and in 1926 Faure (*8, pp. 72-75*) gave notes on the biology of the same species, figuring the adult, the full-grown larva, and the head and mandible of the full-grown larva.

Nothing has been published on the biology of *B. compsilurae*, but in 1934 Proper (*22*) noted it as a parasite of several tachinid flies, giving percentages of puparia infested.

BRACHYMERIA INTERMEDIA (NEES)

DISTRIBUTION AND HOST RELATIONSHIPS

Brachymeria intermedia is well distributed throughout southern Europe and northern Africa. Rearings of gypsy moth material in connection with the work of the Bureau of Entomology show recoveries from Portugal, Spain France, Italy, Hungary, Czechoslovakia, Yugoslavia, and Algeria. De Lépiney (*12*) records it from Morocco, Chorbadzhiev (*2*) from Bulgaria, Masi (*14, pp. 78–82*) from Rumania, Ruschka (*26*) from Turkey and East Bokhara, and Sacharov (*27*) from southern Russia (Astrakhan).

B. intermedia is perhaps best known as a parasite of *Porthetria dispar*. It is, however, very polyphagous, attacking many species of lepidopterous pupae and at least one species of hymenopterous cocoon. Under laboratory conditions it has also been reared from several species of tachinid puparia. In the literature it has only been recorded as a parasite of lepidopterous pupae. A list of the recorded host species follows:

Aporia crataegi L. (*26*)
Hypogymna morio L. (*26*)
Malacosoma neustria L. (*9, 23*)
(*Oenophtheria*) *Sparganothis pilleriana* Schiff. (*26, 30*)
Papilio podalirius L. (*26*)
Pieris daplidice L. (*27*)[4]
Pieris rapae L. (*27*)
Polia oleracea L. (*15*)
(*Tmetocera*) *Eucosma ocellana* F. (*13, 28*)
Tortrix pronubana Hbn. (*3*)
Tortrix viridana L. (*3, 9, 28*)
Zygaena angelicae O. (*26*)
Zygaena ephialtes L. (*26*)
Zygaena filipendulae L. (*13, 14, 26, 28*)
Zygaena transylvanica Burgeff (*13, 14, 28*)

During the present study it has been reared from pupae of *Vanessa io* L., and also from cocoons of the hymenopterous parasite *Rogas unicolor* Nees. *R. unicolor* is a parasite of *Stilpnotia salicis L.* in central Europe. Its cocoon is formed within the larval skin of the host, which becomes a dry, taut case. Adults issue in from 10 to 14 days after formation of the cocoon, and during this period it is exposed to the attack of hyperparasites. In 1933, 2,254 *Rogas* cocoons were collected in Budapest, Hungary, and 2 of them produced *B. intermedia*. In 1934, 4,869 *Rogas* cocoons were collected, and *B. intermedia* issued from 12 of them.

A study of the host relationships of *B. intermedia* was made under laboratory conditions at Budapest, Hungary, by exposing to attack numerous lepidopterous pupae, tachinid and sarcophagid puparia, and hymenopterous cocoons. Practically any naked lepidopterous host pupa was attacked, although hairy pupae, such as *Stilpnotia salicis*, were refused. All hymenopterous cocoons were refused, and sarcophagid puparia were apparently too hard for the females to pierce. Tachinid puparia, on the other hand, were readily attacked, especially when fresh. A list of host species in which *B. intermedia* was reared in the laboratory follows:

Lepidoptera:
Abrostola triplasia L.
Acronycta tridens Schiff.
Cadonia punctoria L.
Cynthia atalanta L.
Mamestra brassicae L.
Nygmia phaeorrhoea Don.
Pieris brassicae L.
Polygonia c-album L.
Lepidoptera—Continued
Vanessa xanthomelas Esp.
Vanessa urticae L.
Diptera (tachnid puparia):
Compsilura concinnata Meig.
Sturmia bella Meig.
Sturmia inconspicua Meig.
Tachina larvarum L.
Tricholyga sorbillans Wied.

[4] Faure (*8, p. 75*) believes Sacharov's species may be *B. femorata* (L.).

Brachymeria intermedia has also completed development in the following American species attacked at the Melrose Highlands laboratory:

Autographa brassicae Riley
Basilarchia archippus Cram.
Cynthia atalanta L.
Euphydryas phaeton Dru.
Hamadryas milberti Godt.
Hemerocampa leucostigma S. and A.
Heterocampa guttivitta Walk.
Lemonias harrisii Scudd.
Papilio glaucus L.

Although *B. intermedia* has been reared from field-collected hymenopterous cocoons, and it readily parasitizes tachinid puparia in the laboratory, the large number of lepidopterous hosts recorded in the literature makes it seem certain that under field conditions it is almost entirely a parasite of that group. Apparently it is rarely a parasite of *Rogas unicolor*. It may attack other species of Hymenoptera, but no such records have been made. Difficulties encountered in collecting tachinid puparia in the field have made it impossible to judge whether *B. intermedia* ever attacks these hosts under natural conditions, but even though it readily attacked and completed development in tachinid puparia that were exposed to it in the laboratory, it is not believed to be normally a parasite of tachinids. Several attempts have been made to induce it to attack tachinid maggots in lepidopterous pupae and larvae, but without success; and since most tachinids form their puparia in the soil, they would be inaccessible to *B. intermedia*.

ECONOMIC IMPORTANCE

Most of the rearing work to obtain parasites of *Porthetria dispar* that has been conducted in Europe by the Bureau of Entomology has been in central European countries, and there *B. intermedia* has been of slight importance as a control factor. Twice, however, it has been observed to be extremely important in more southern rearing points. In 1911 W. F. Fiske [5] made large shipments of parasites from a heavy infestation of *P. dispar* at Caltagirone, Sicily. He considered *B. intermedia* one of the best parasites at that point, noting that 4 or 5 adults could be observed flying around each tree. He gave no figures on the percentage of pupae parasitized, but he had 44,000 "parasitized" pupae and 12,000 adults collected, and these figures indicate that the species must have been plentiful. In 1927 R. T. Webber [5] conducted rearing work in a forest at Oran, Algeria. He considered it "undoubtedly the most important parasite" in that forest. A collection of 100 host pupae yielded no less than 26 *B. intermedia*. Pupae that were shipped to the United States from Oran unfortunately suffered severe mortality; so it was impossible to estimate the degree of parasitization of a large number of pupae. In 1930 De Lépiney (*12, p. 87*) gave a detailed account of a study of *P. dispar* in the forest of Mamora in Morocco. He makes the following remarks regarding *B. intermedia*.

> *Chalcis intermedia* was of primary importance in certain regions of the forest in 1924 and 1925. In 1925 nearly all the pupae along the Salé-Tiflet road in the region designated as "promontory A", which was totally defoliated, were parasitized, so that *P. dispar* was rarely seen in 1926; total defoliation was not observed again in that region until 1928. But since 1925 *Chalcis intermedia* has practically disappeared, not only on promontory A, but throughout the whole forest; only a few specimens having been found.

[5] Unpublished notes at the Melrose Highlands laboratory.

Rearing work has also been conducted in Spain and Portugal. The climate of these countries is probably suited to *B. intermedia*, but the parasite was of minor importance during the 2 years in which collections were made. In 1924, 7,683 *P. dispar* pupae were collected in Spain, and 315 *B. intermedia* adults were recovered. In 1925, 957 *B. intermedia* adults were reared from 25,000 host pupae collected in Spain, and 1,433 from 51,900 pupae collected in Portugal.

From these facts we may conclude that *B. intermedia* occurs generally as a parasite of *P. dispar* in the Mediterranean countries, and that at times it becomes of primary importance as a control factor. Apparently, however, it does not thrive in the colder climate of central Europe, where the mortality among overwintering adults probably is very high. This seems to be equally true in New England for, although more than 20,000 adults have been liberated, the parasite has failed to establish itself in spite of the fact that it has been reared in the laboratory on various American host species.

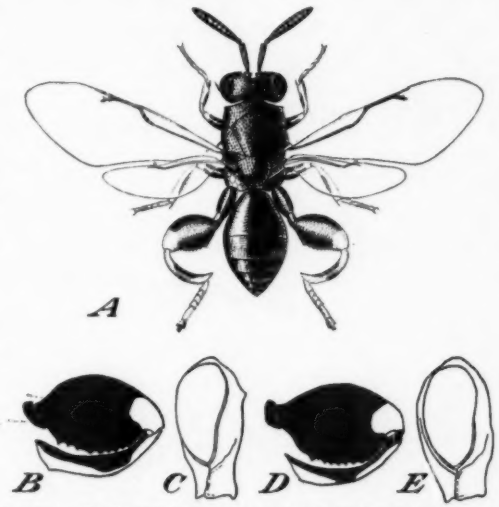

FIGURE 1.—*Brachymeria intermedia: A*, Adult (from Howard), (× 6); *B*, adult female, hind femur and tibia, showing markings (from Crawford) (× 11); *C*, head, showing carina at front of malar space (from Crawford) (× 15). *B. compsilurae: D*, adult female, hind femur and tibia, showing markings (× 11); *E*, head showing carina at front of malar space (× 15).

Sacharov (*27*) found *B. intermedia* [6] to be an important parasite of the mustard feeder, *Pieris daplidice* L. In 1911 it was responsible for the destruction of about 50 percent of the pupae of this species where studies were conducted in the Government of Astrakhan in southern Russia.

THE ADULT

(*Chalcis*) *Brachymeria intermedia* (fig. 1, *A*) was first described by Nees in 1834 (*16, pp. 29–30*). Masi (*14, pp. 78–82*) redescribed it in 1916, and Ruschka (*26*) wrote a redescription in 1922. Crawford (*5*) keyed the species (under the name *Chalcis flavipes* Panz.) in 1910, and his figures of the "hind femur and tibia, showing markings" and "head, showing carina at front of malar space", are reproduced in figure 1, *B* and *C*.

THE EGG

The newly laid egg (fig. 2, *B*) is 0.90 mm long and 0.20 mm wide. It is slightly curved with rounded ends, being somewhat wider at

[6] See footnote 4, p. 497.

the cephalic end. The chorion is smooth and hyaline except for a slightly roughened area at the micropyle. The embryo is semi-opaque and grayish in color.

THE FIRST-INSTAR LARVA

The first-instar larva is strikingly different from that of *Brachymeria compsilurae* Cwfd. It closely resembles ectoparasitic forms in

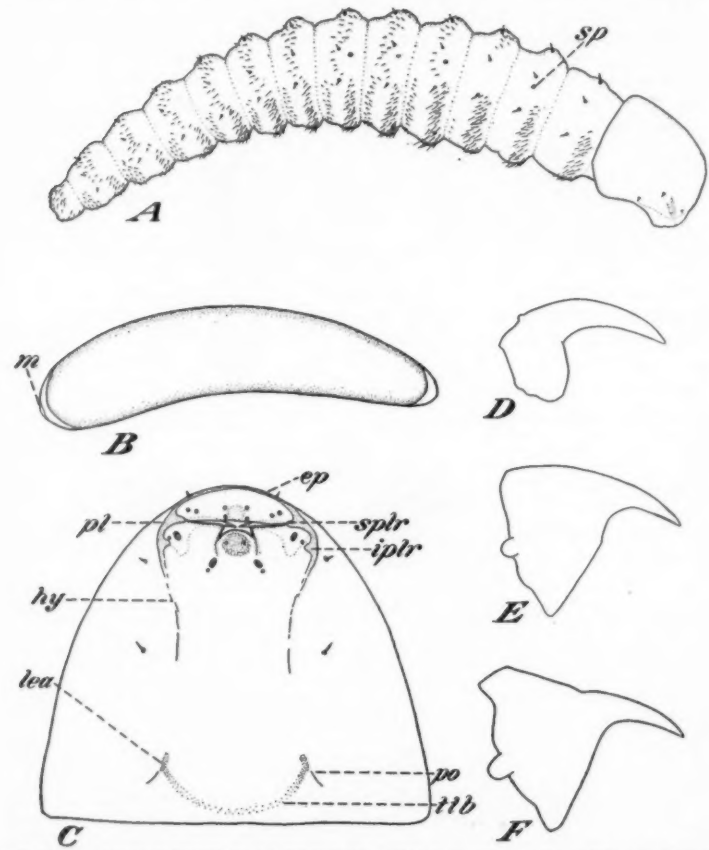

FIGURE 2.—*Brachymeria intermedia: A*, First-instar larva (× 92); *sp*, spiracle. *B*, Egg (× 67); *m*, micropyle *C*, Head of first-instar larva, ventral aspect (× 275); *ep*, epistoma; *spltr*, superior pleurostomal ramus; *pl*, pleurostoma; *ipltr*, inferior pleurostomal ramus; *hy*, hypostoma; *lea*, lateral epicranial angles; *po*, postocciput; *ttb*, transverse tentorial bar. *D*, First-instar mandible (× 500). *E*, Second-instar mandible (× 428). *F*, Third-instar mandible (× 300).

having 13 well-differentiated segments, and is tapered posteriorly. It belongs to Parker's group 6 (*20*).

The newly hatched larva measures about 1.08 mm long and 0.23 mm wide, with body form as shown in figure 2, *A*. The head is well defined, and there are 13 body segments about equal in length. Each

segment bears a number of cuticular spines (fig. 3, *C*), and all except the last have 3 pairs of sensory setae (fig. 3, *B*) placed as follows: 1 just above the line of spiracles, 1 near the dorsal margin of the segment, and 1 just below the median line. Possibly the last abdominal segment has sensory setae, too, but none could be distinguished. The sensory setae are much like the cuticular spines, especially on the posterior segments. Below the median line the spines on the anterior portions of the segments are directed backward

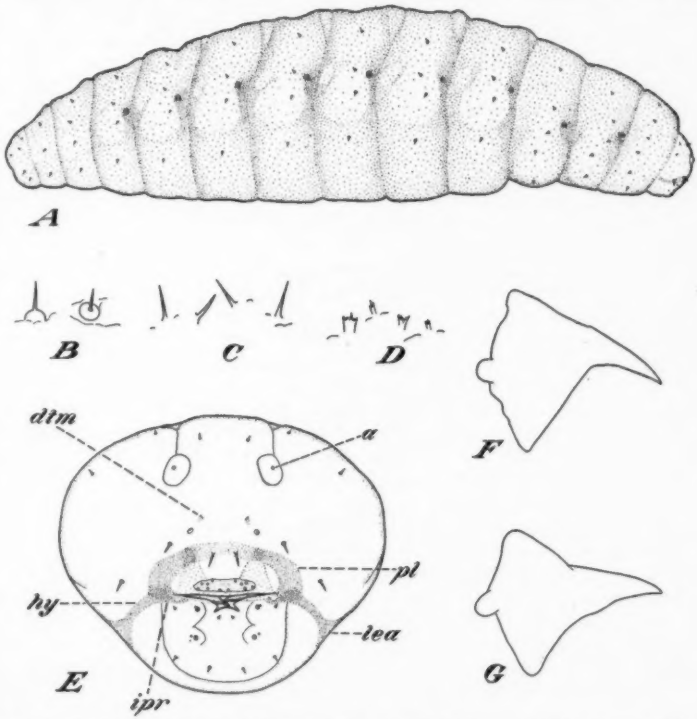

FIGURE 3.—*Brachymeria intermedia: A*, Full-grown larva (× 10). *B*, Sensory setae (× 400). *C*, Cuticular spines (× 400). *D*, Compound cuticular spines of last abdominal segment, fourth instar (× 400). *E*, Head of full-grown larva; *a*, antenna; *dtm*, dorsal tentorial macula; *pl*, pleurostoma; *hy*, hypostoma; *ipr*, inferior pleurostomal ramus; *lea*, lateral epicranial angles (× 50). *F*, Fourth-instar mandible (× 200). *G*, Fifth-instar mandible (× 120).

and those on the posterior portions are directed forward. Above the median line all the spines are directed backward. The last abdominal segment differs from the others in having no well-defined groups of spines, although spines are scattered over the entire surface, all of which are directed backward.

The head is thimble shaped and lightly sclerotized (fig. 2, *C*). It bears a pair of short truncate antennae. The mouth opening is on the ventral side at the apex. The mandibles (fig. 2, *D*) are 0.05 mm long. They are sickle shaped, well sclerotized, and yellow at the tips. There is a skeletal crossbar (not shown in the illustration) connecting the inferior pleurostomal rami and extending across the

mouth opening just below the mandibles. Phillips (*21*) calls this crossbar the "hypopharyngeal bracon." The hypostoma is weak except at the epicranial angles and just below the pleurostoma, the postocciput is poorly defined, and the transverse tentorial bar is weakly sclerotized.

The tracheal system is composed of a pair of lateral longitudinal trunks united anteriorly in the first thoracic and posteriorly in the ninth abdominal segment. There are 4 pairs of open spiracles, a pair on the second thoracic and on each of the first 3 abdominal segments. They measure 0.006 mm in diameter. Rudimentary spiracular branches are present in the third thoracic and the fourth to seventh abdominal segments, although there are no open spiracles on these segments. The spiracular branches give rise to several dorsal branches in each segment, as well as several that are directed ventrally. The main ventral branches arise from the longitudinal trunk near the base of the spiracular branches. These subdivide into many smaller branches. The head is supplied from branches arising in the first thoracic segment, and the last abdominal segment receives branches from the longitudinal trunks in the ninth abdominal segment.

The digestive system is well developed at the time of hatching. The fore-intestine extends to the middle portion of the first thoracic segment, where it empties into the mid-intestine, or stomach. The mid-intestine occupies most of the body cavity, extending back to the anterior portion of the eighth abdominal segment, where it joins, but does not open into, the hind-intestine. The hind-intestine has a narrow anterior portion, to which the malpighian tubes are attached, and a wider, urn-shaped rectum. The salivary glands are conspicuous tubes lying on each side of the body. They unite in the posterior portion of the head into a common duct which opens on the floor of the mouth. The tubes are nearly straight in the first two thoracic segments, but they then become strongly serpentine, making a large curve in each segment as far back as the seventh abdominal, where they straighten out and extend along the venter of the eighth abdominal segment, turning upward and terminating in the ninth. There are two pairs of malpighian tubes connected to the base of the hind-intestine. A short, but strongly sinuous dorsal pair extends backward into the last segment. The other pair are long tubes extending anteriorly just above the salivary-gland tubes. They are attached to the hind-intestine just below the dorsal pair; from this point they curve upward and then extend in a nearly straight line to the third thoracic segment.

The brain and nerve cord are distinct. The latter is relatively wide, with only slight swellings at the ganglia. It extends to the seventh abdominal segment, where the last 2 pairs of ganglia are fused, giving off 2 pairs of nerve fibers.

The dorsal blood vessel extends from the head to the ninth abdominal segment. It is a muscular, tubelike organ lying along the dorsal wall. It is difficult to distinguish in the first instar, but may be seen readily in older larvae.

THE SECOND-INSTAR LARVA

Second-instar larvae are from 2.00 mm long and 0.53 mm wide to 2.86 mm long and 0.88 mm wide. They are similar to the first-instar

larvae, but are readily distinguished by the shape of the mandibles and the size of the spiracles. The mandibles (fig. 2, *E*) are not much larger than those of the first instar, measuring only 0.06 mm, but they are less heavily sclerotized and have much broader bases. The spiracles of the second thoracic segment are 0.015 mm in diameter. The stumps of rudimentary spiracular branches in the third thoracic and fourth to seventh abdominal segments are more pronounced than in the first instar, and in the head the hypostoma and the postocciput are more clearly defined. Otherwise the two instars seem to be identical. The internal anatomy is similar to that of *B. compsilurae*, which is shown in figure 5, *A*.

THE THIRD-INSTAR LARVA

Third-instar larvae are from 2.7 mm long and 0.66 mm wide to 3.80 mm long and 1.04 mm wide. The larval form is the same as in the previous instars, but it is distinctly more robust, and the head is wider. The arrangement of the sensory setae is the same as in the first instar. Three pairs were distinguishable on the last abdominal segment, 2 on the dorsal surface and 1 on the ventral. The cuticular spines have practically the same arrangement as before. There are fewest in the dorsal and pleural regions of the segments, and the groups on the posterior portions of the abdominal segments are wider than those on the anterior portions. The last abdominal segment has spines scattered over the dorsal surface, but very few on the ventral surface. The direction of the spines is as before.

The head is like that of the full-grown larva except that it is much smaller and less heavily sclerotized. The tiny spines and sensoria can now be distinguished readily. The mandibles (fig. 2, *F*) are much larger, measuring 0.103 mm, but they closely resemble those of the second instar.

The tracheal system has 9 pairs of open spiracles, 1 pair each on the mesothorax and the metathorax and a pair on each of the first 7 abdominal segments. The mesothoracic spiracle is 0.023 mm in diameter. The eighth abdominal segment has a closed spiracular branch.

The digestive, nervous, and circulatory systems are the same as in the first instar. The mid-intestine, which is clearly visible through the skin, usually exhibits 1 or 2 conspicuous, round vacuoles.

THE FOURTH-INSTAR LARVA

Fourth-instar larvae are from 4.0 mm long and 1.0 mm wide to 6.0 mm long and 1.5 mm wide. They show only minor differences from the preceding instar. The mandibles (fig. 3, *F*) still have the same shape, but they measure 0.15 mm. The mesothoracic spiracles are 0.04 mm in diameter. There are the same number of sensory setae as in the full-grown larva, and their arrangement is the same. The cuticular spines are situated as before, but there are almost none in the pleural and dorsal regions of the first nine segments. The tenth segment has a few in the dorsal region, the eleventh and twelfth segments have them on both dorsal and pleural regions, and the last segment has them on the dorsal surface only.

In the other instars almost all the cuticular spines are straight and have a single point (fig. 3, *C*), although occasionally a spine having

two points is noted. In this instar, however, many of the cuticular spines on the last abdominal segment have several points (fig. 3, *D*).

THE FIFTH-INSTAR LARVA

The full-grown or fifth-instar larva (fig. 3, *A*) has the same general form as the freshly hatched larva. The measurements of individuals range from 6.75 mm long and 2.0 mm wide to 11.5 mm long and 3.0 mm wide. The mesothoracic and metathoracic spiracles and lateral lobes are distinctly lower than the line of spiracles and lateral lobes of the abdominal segments. The mesothoracic spiracles are 0.08 mm in diameter. There are no cuticular spines. The number and arrangement of the sensory setae are indicated in the figure. The first thoracic segment has 6 pairs, the second and third thoracic segments have 5 pairs each, the first 8 abdominal segments have 4 pairs each, the ninth abdominal segment has 3 pairs, and the last abdominal segment has 3 pairs on its dorsal surface and 2 pairs on its ventral surface. The number of sensory setae varies, particularly on the last segment, although most of the specimens examined have the numbers given. Possibly difficulties connected with preparing specimens and locating these minute spines account for the slight variations noted.

The head, seen from the front, presents well-defined characters (fig. 3, *E*). The mandibles (fig. 3, *G*) are 0.22 mm long and 0.19 mm broad. They are very broad and funnel shaped at the base, with heavily sclerotized, reddish brown tips. The inferior pleurostomal rami are connected by a stout crossbar, the hypopharyngeal bracon, extending across the mouth opening just below the mandibles. The transverse bridge of the tentorium is strongly developed, extending across the head between the lateral epicranial angles. There are two distinct dorsal tentorial maculae present on the frons, but no connection between them and the tentorium can be distinguished. Just below each of these marks a tiny oval elevation with a light spot at its center may be noted. These are probably sensoria. The antennae are small nipplelike protuberances surrounded by large oval areas, the antennal foramina. Indistinct sutures lead from the antennal foramina to slight troughlike indentations of the apex of the occiput.

The tracheal system is essentially the same as in the preceding instars, but the branches are much larger and more ramified.

The digestive system is like that of the first instar. Parker (*20, fig. 251*) has figured the digestive system of *Brachymeria fonscolombei*, which is very similar, although the mid-intestine of *B. intermedia* is less oval and the hind-intestine is much longer and stouter.

The nervous system consists of the brain, the subesophageal ganglia, and the ventral nerve cord. The ventral nerve cord bears 11 pairs of ganglia, which are separated from each other by two heavy fibers. Each ganglion gives off a long nerve fiber, which may transverse several segments. The last ganglion probably represents 2 pairs united, for it gives off 2 pairs of branches. The point of termination of the nerve cord seems to depend on the larval development. In some large prepared specimens it extended to the fourth, and in smaller specimens to the sixth, abdominal segment.

The histoblasts, or imaginal buds, are easily distinguished in this instar. They are white and semiopaque, and lie just beneath the

cuticle. The antennal histoblasts are situated in the antennal rudiments, the leg and wing histoblasts ventrally and laterally in the thoracic segments, and the histoblasts of the genitalia are located ventrally in the eighth and ninth abdominal segments in the female and in the ninth abdominal segment in the male.

The fat body is conspicuous in this instar. It consists of several rows of large oval cells placed between the skin and the integumentary muscles of each segment.

THE PREPUPA

The full-grown larva voids its meconium almost immediately after becoming full fed, and the prepupa may be observed through the loosely fitting larval skin. The prepupa is pure white. At first only the head and thorax can be distinguished, but later the abdomen and appendages of the head and thorax can be differentiated.

THE PUPA

The pupa has a thin, closely fitting, transparent skin, through which the forming adult characters can be clearly distinguished. At first it is yellowish, but as development proceeds pigmentation takes place rapidly and it becomes shiny black.

SEASONAL HISTORY

Brachymeria intermedia overwinters as an adult. Two generations, and possibly a partial third, are completed during the summer months; nevertheless, first-generation females may hibernate successfully.

The adults probably hibernate under the bark of dead trees or in similar places. In the laboratory they remain motionless along the sides or in the corners of the boxes provided for them, but they have never been observed to enter the soil.

At Budapest, Hungary, the insects become active and feed a little during March and April. Attempts were made there to get them to oviposit as soon as possible, in order to determine whether the species went through a generation before attacking *Porthetria dispar*. No eggs were deposited until May 15, when one pupa was apparently attacked, but between May 15 and 25, eggs were deposited in more than 50 preferred-host chrysalids. None of this material, however, produced adults of *B. intermedia*. Seven chrysalids of *Vanessa xanthomelas* were oviposited in on June 7, and from these eggs four *B. intermedia* were reared. Since by this time *P. dispar* pupae are often present in the field in Hungary, it is undoubtedly one of the first species attacked. The first adult *B. intermedia* reared from field-collected *P. dispar* pupae issued on June 28, and issuance continued until July 25. These first-generation adults eagerly attacked a variety of host species during July, August, and September, and second-generation adults began to issue late in August. A second generation is evidently produced under field conditions also, for two *B. intermedia* adults were reared from chrysalids of *Vanessa io* collected at Olaszliszka, Hungary, on August 12, 1926, the adults issuing on September 16 and 20. The second-generation adults that were reared in the laboratory practically refused to oviposit, although they finally did attack some retarded *P. dispar* pupae, and a third generation was reared. It seems questionable, however, if a third generation would develop in the field. Adults of the third generation could not be induced to oviposit.

In New England the seasonal history of *B. intermedia* would probably be somewhat different, for here *Porthetria dispar* completes development much later than it does in central Europe. Pupae are present in the field from about July 5 to August 10, and laboratory rearing indicates that there would be time for *B. intermedia* to complete a generation on other hosts before many *P. dispar* pupae are available. The first host pupae to be parasitized successfully at the Melrose Highlands laboratory were those of *Heterocampa guttivitta* attacked on May 21. A number of host species were attacked during May and the first half of June, and first-generation adults began to issue by June 30 and continued issuing until July 20. It seems probable that these adults would normally attack *P. dispar* pupae available in the field and that second-generation adults would issue during August and September. Whether or not a third generation would develop is questionable. It is known, however, that first-generation adults sent here from Europe attack various American host species in August and September. Therefore, if second-generation adults were issuing from American *P. dispar* at this time, they would probably attack available host species, thus producing a third generation.

HABITS OF THE ADULT

The adult *Brachymeria intermedia* emerges from the host pupa after chewing an irregular hole in the pupal shell. A count of 82 pupae showed 40 exit holes in the anterior end, 37 near the middle, and 5 near the posterior end. Their swollen femora give the adults a clumsy appearance as they slowly move around in confinement, but in nature they are very graceful fliers. Both sexes thrive when confined in glass-topped wooden boxes or cloth-covered cages and fed dry lump sugar and a honey solution (1 part honey to 5 parts water) held on sponges. The cages are kept in a dark, cool place when the insects are not being used. The females live through the winter, but the males die. Difficulty has been experienced in getting the females to hibernate, but most of those that did survive the winter lived well into the summer. A record of 113 hibernated females that issued between July 22 and August 5 of the previous year showed that the first female died on June 18 and the last on August 9, and there was no heavy mortality until the last part of July.

Adults of *B. intermedia* mate readily in confinement. Cloth-covered cages containing several males are placed in the direct sunlight, and a few females are introduced. As the females are mated they are removed, for they mate only once, and the males will continue to pursue them if they are left in the cages. High temperature at midday is the optimum condition, and mating is encouraged if the cage is taken to a shady place after it has been held in the sunlight for about 10 minutes. The time spent in coitu is from 30 to 40 seconds. The age of females seems to be of little importance in mating. Females up to 6 days old mate readily. One female 8 days old was mated in the laboratory, and a few unmated females that hibernated were mated with first-generation males the second summer.

As a rule females do not oviposit readily until 2 or 3 days after mating. Two females were observed to oviposit immediately after fertilization, but no parasites were reared from the eggs. The female crawls onto a host pupa and slowly walks over it a few times. Suddenly she takes a firm grasp on her victim with her powerful hind legs

and, extending her ovipositor, inserts it slowly in the rigid head end of the pupa. The pupa writhes violently, but the parasite shows remarkable ability to hang on as the host rolls around. Oviposition lasts from 40 seconds to 3 minutes. At the end of this time the ovipositor is withdrawn and the host becomes quiet. A small drop of fluid sometimes exudes from the puncture hole, and this the parasite often consumes.

Attempts to determine how many eggs a single female lays were not very satisfactory At best, oviposition is very slow, and females that were confined individually did not oviposit so frequently as they are believed to do in nature. One female, which laid 48 eggs, was dissected after death, and the ovaries were found to contain a number of well-developed eggs. Apparently they do not lay more than about 6 eggs per day. It was repeatedly noted that 5 females, caged together, would lay 25 or 30 eggs and then show no further interest in host material during that day, and isolated females never laid more than 7 eggs in a single day. An examination of the female reproductive system showed that this is undoubtedly normal. The ovaries have only 3 ovarioles, and, since the eggs are rather large when laid, each ovariole holds only 1 well-developed egg at a time.

Unmated females of *B. intermedia* will oviposit readily, and only males are produced in parthenogenetic reproduction.

No satisfactory records have been kept on the proportion of sexes issuing from field-collected material. In 1930, 2,076 adults were recovered from *Porthetria dispar* pupae collected in Platicevo, Yugoslavia; of these, 682 were males and 1,394 were females. That year, however, the host pupae were held in the field until the first *B. intermedia* adults issued, and probably some males were lost. Experiments in reproduction conducted at the laboratory gave contradictory results. In 1927 mated females that had been reared from *P. dispar* pupae collected in Algeria attacked a number of *P. dispar* pupae on arrival at Melrose Highlands. A total of 228 adult *Brachymeria* were reared, with equal numbers of males and females. In 1930 mated females that had been reared from *P. dispar* pupae in central Europe were used, and 184 adults were reared, but only 26 were males.

TABLE 1.—*Hibernation of Brachymeria intermedia females in 1930 and 1932*

History of material	Box no.[1]	Adults placed in hibernation	Adults successfully hibernating
		Number	*Number*
First-generation females not used in fall reproduction	1	50	33
	2	50	23
	3	50	32
	4	60	16
First-generation females used in fall reproduction	5	50	32
	6	50	27
	7	50	30
	8	38	10
Second-generation females not used in fall reproduction	9	51	50
	10	30	25
Unmated females not used in fall reproduction	11	55	12
	12	50	28

[1] Boxes nos. 4, 8, and 11 show hibernation records for 1932; all others show hibernation records for 1930.

So much difficulty was experienced in getting *B. intermedia* adults to hibernate under laboratory conditions that it is believed that there must be rather high mortality in the field. Prior to 1930 so few in-

dividuals lived through the winter that figures are hardly significant. In 1930 and 1932, however, material was held in an unheated insectary in glass-covered wooden boxes measuring 9 by 5 by 3½ inches, and the results were more satisfactory. The records are given in table 1.

The data in table 1 show that first-generation females that oviposit in the fall live through the winter just as well as those that do not oviposit and almost as well as second-generation females. In 1930 the second-generation females hibernated considerably better than those of the first generation, but in 1932 there was little difference. In 1933 it was found that successfully hibernated females that oviposited in the fall of 1932 oviposited almost as well as females that had not previously laid eggs.

DEVELOPMENT OF IMMATURE STAGES

The egg of *Brachymeria intermedia* remains about where it is laid, in the body of the host pupa. It hatches in about 48 hours, and the young larva starts feeding immediately. The larva (fig. 2, *A*) is remarkably similar to most externally feeding chalcidoid larvae, although it seems to be a true internal feeder.

One of the first activities of the primary larva is the elimination of competitors. Only one parasite ever completes development in the same host pupa, and, although many very young dead larvae have been found in a host, no more than one living well-fed first-instar larva has ever been discovered. Possibly, as in many parasitic Hymenoptera, actual combat between the young larvae is not necessary to cause death, but all dead larvae of this species that have been found bear marks of mandibles, and when living larvae are dissected out of the host pupa and placed together they quickly engage one another.

The young larva develops rapidly and by the end of the second instar has taken up a position on the venter of the host pupa near the junction of the wing covers and the abdominal segments. Here it feeds on the host contents until, by the time it is full grown, most of the anterior portion of the pupa has been eaten out and is occupied by the parasite. *B. intermedia* frequently parasitizes a pupa that contains much more food than is necessary for its development. This surplus remains, gradually drying up. The larva casts its meconium almost immediately after becoming full grown, and prepupal and pupal development follow. The larva usually finishes feeding with its anterior end toward the head of the pupa, and the adults emerge from the anterior end or from the center of the pupal shell.

The time required for development from egg to adult varies greatly with the temperature. *Vanessa urticae* chrysalids attacked on July 31 produced adults of *B. intermedia* in 18 days, but retarded *P. dispar* pupae attacked on September 11 produced *B. intermedia* adults in from 51 to 62 days. A large number of dissections during the normal season of development on *P. dispar* indicate rather clearly, however, that the average time in each stage is as follows: About 2 days in the egg stage, 2 days in each of the first four larval instars, 3 days in the last larval instar, 2 days as a prepupa, and 13 days as a pupa, making a total of 28 days. Females require about 2 days longer for development than males.

FACTORS LIMITING THE EFFECTIVENESS OF THIS PARASITE

There are a number of factors that limit the effectiveness of *Brachymeria intermedia* as a parasite of *Porthetria dispar*. In the

first place, it overwinters as an adult and apparently cannot withstand the rigorous climate that this host endures in central Europe and in New England. It has been extremely important in Sicily and northern Africa, where the winters are mild, but in central Europe it has been difficult to get the parasite to hibernate, and, although it persists in that region and can complete development in a number of hosts, it remains of minor importance. New England has about the same climate as central Europe. *B. intermedia* can develop in a number of American species, but it has never become established in spite of the large colonies of adults that have been liberated. If the gypsy moth or other suitable host were to become established in the southern part of the United States, *B. intermedia* would probably become established there, whereas in New England climatic conditions are unsuitable for its existence.

There must be other factors limiting the effectiveness of *B. intermedia* to account for its sudden disappearance from the forest of Mamora in Morocco, as described by De Lépiney (*12*). It is difficult, and perhaps unwise, to hazard a theory regarding this phenomenon. It nevertheless seems as though the fact that *B. intermedia* passed through a second generation on some other host might explain this, for, of course, the second-generation host would have to be present in some numbers for the parasite to maintain itself. In any case, the fact that the parasite may require another host species might limit its effectiveness against *P. dispar*.

BRACHYMERIA COMPSILURAE (CWFD.)

DISTRIBUTION AND HOST RELATIONSHIPS

Brachymeria compsilurae is a North American species which has been taken in northwestern Wisconsin, northeastern Pennsylvania, New Jersey, New York, and all the New England States. Its known range will probably be extended as additional rearing records are obtained.

So far as is known, *B. compsilurae* acts solely as a parasite of tachinid flies. A list of tachinids from which *B. compsilurae* has been reared, with their primary lepidopterous hosts, follows. The species that are starred (*) were attacked under laboratory conditions.

Tachinid Host of *B. compsilurae*	Lepidopterous Host of Tachinid from Which *B. compsilurae* Was Reared
Achaetoneura aletiae Riley.	*Hemerocampa leucostigma* S. and A.
Achaetoneura frenchii Will.	*Melalopha inclusa* Hbn.
Carcelia laxifrons Vill.	*Nygmia phaeorrhoea* Don.
Compsilura concinnata Meig.	*Porthetria dispar* L. *Nygmia phaeorrhoea* Don. *Stilpnotia salicis* L. *Hemerocampa leucostigma* S. and A. *Hamadryas antiopa* (L.). **Bombyx mori* L. **Euchaetias egle* Dru.
Pelatachina pellucida Coq.	*Hamadryas antiopa* (L.).
Phorocera agilis R. D.	**Porthetria dispar* L.
Phorocera claripennis Macq.	*Hemerocampa leucostigma* S. and A.
Sturmia nidicola Towns.	*Nygmia phaeorrhoea* Don.
Sturmia scutellata R. D.	*Porthetria dispar* L.
Tachina mella Walk.	*Hemerocampa leucostigma* S. and A.
Zenillia ampleza Coq.	*Hemerocampa leucostigma* S. and A.

The hosts of *B. compsilurae* are attacked in the larval stage, while still within the larval skin or pupa of the primary host. The diversity of the lepidopterous hosts indicates that *B. compsilurae* will oviposit through a wide variety of integuments, and, since it has been found to complete development in so many species of Tachinidae, the actual number of host species which it may parasitize is undoubtedly extremely large.

ECONOMIC IMPORTANCE

Without doubt *Brachymeria compsilurae* parasitizes large numbers of tachinid parasites, retarding their rate of increase and thus seriously limiting their effectiveness. Two of the most important species that it is known to attack severely are *Compsilura concinnata* and *Sturmia scutellata*. Both these flies have been introduced from Europe in the campaign against the gypsy moth. *C. concinnata* is one of the most effective parasites of the gypsy, brown-tail, and satin moths, and *S. scutellata* is one of the most effective parasites of the gypsy moth. *B. compsilurae* is therefore of considerable economic importance as affecting the biological control of these pests.

B. compsilurae attacks its various host species when they are in the larval stage, and the parasite issues from the host puparium. An accurate estimate of the degree of parasitization of any host would therefore have to be based upon an examination of representative samples of puparia collected under field conditions. Unfortunately, however, even when large numbers of Tachinidae are known to be present, it is exceedingly difficult to collect puparia in the soil. A few collections have been made, but most of the records have been taken from puparia formed after the primary lepidopterous host was collected, i. e., when the tachinids were still in the larval stage inside their host. Obviously these tachinid larvae were not exposed to *B. compsilurae* so long as they would have been under natural conditions, and since *B. compsilurae* oviposits most readily when the tachinid maggots are full grown, the percentage of parasitization of this stock is probably lower than in material remaining in the field.

Collections made to obtain records on the prevalence of *Brachymeria compsilurae* fall into four categories. The first consists of a large number of *Sturmia scutellata* puparia obtained over a period of 4 years throughout the area in New England infested with *Porthetria dispar*, in connection with experiments on attractants for male gypsy moths (Collins and Potts, 4). In these experiments female gypsy moth pupae were collected and held on racks until the moths issued. Large numbers of *S. scutellata* maggots issued from these *P. dispar* pupae. Additional puparia were obtained from miscellaneous collections of *P. dispar* material received at the laboratory. The second type of collection consists of several small lots of *S. scutellata* obtained by collecting *P. dispar* pupae at various points. The collections at each point were kept separate in order that the importance of *B. compsilurae* at widely separated points might be judged. In the third type of collection [7] *P. dispar* pupae were collected and left in the forest, in order that the *Sturmia* maggots might be exposed to *B. compsilurae* under field conditions, but that the recovery of puparia might be facilitated by concentration. In spite of these conditions, however, few puparia were found. The fourth type of collection includes four lots of *Compsilura*

[7] This work was done by T. H. Jones, of the Melrose Highlands laboratory.

concinnata puparia that were taken from the field. Table 2 gives the results of these collections in detail.

TABLE 2.—*Brachymeria compsilurae reared from various lots of tachinid puparia*

Type of collection	Place collected	Year	Total puparia recovered	Flies	Dead from unknown cause	*Brachymeria compsilurae* reared	*Brachymeria* from total puparia
			Number	*Number*	*Number*	*Number*	*Percent*
STURMIA SCUTELLATA							
(1) *Porthetria dispar* pupae	Generalinfestedarea.	4 years	24,070	11,586	10,546	1,938	8.1
(2) Special collections of *P. dispar* pupae.	Ossipee, N. H.	1932	879	544	213	122	13.8
	Francistown, N. H.	1933	494	400	20	74	14.9
	Sebago, Me.	1933	292	213	27	52	17.8
	Middleboro, Mass.	1933	197	182	7	8	4.0
	Westford, Mass.	1934	382	221	70	91	23.8
	Foxboro, Mass.	1934	126	18	64	44	34.9
(3) *P. dispar* pupae left in forest.	Boxford, Mass.	1927	34	15	17	2	5.8
	Middleboro, Mass.	1927	96	46	26	24	25.0
	Boxford, Mass.	1928	31	13	13	5	16.1
	Saugus, Mass.	1928	129	48	73	8	6.2
	Nashua, N. H.	1929	16	6	8	2	12.5
	Boxford, Mass.	1929	10	7	0	3	30.0
	Dighton, Mass.	1930	149	45	55	49	32.8
	Middleboro, Mass.	1932	98	45	22	31	31.6
COMPSILURA CONCINNATA							
(4) Field-collected *Compsilura concinnata* puparia:							
(*a*) In brown-tail moth infestation.	Hampton, N. H.	1924	255	40	[1] 208	3	1.1
(*b*) In gypsy moth infestation.	Marion, Mass.	1933	163	11	[1] 40	112	68.7
	Westford, Mass.	1934	41	11	[1] 11	19	46.3
	Cranston, R. I.	1934	432	34	[1] 144	254	58.7

[1] Most of dead killed by another parasite.

The record shows considerable variation, with a rather high average abundance of *B. compsilurae*. The most interesting collections are the four lots of field-collected *Compsilura concinnata* puparia (type 4). The lot from Cranston, R. I., was collected a little too late in the season, for between 50 and 60 puparia were found from which adult flies had already emerged. The low percentage of *B. compsilurae* from *C. concinnata* collected in Hampton is probably due to the activities of another secondary parasite, *Monodontomerus aereus* Walk. This species regularly attacks *C. concinnata* puparia in brown-tail moth cocoons, drilling through the puparia with its ovipositor. Laboratory experiments show that it will develop just as readily on *B. compsilurae* as on *C. concinnata*. The year that this collection was made *M. aereus* was very abundant, killing almost all the *Compsilura*.

The number of *B. compsilurae* reared from *Sturmia* puparia that were dug up after exposure in the forest (type 3) should represent nearly natural conditions. Considerable variation in the degree of parasitization is noted, and in some lots it was very high.

The large general collections (type 1) represent such a representative sample that if the tachinid larvae had been subjected to the same exposure to attack as under normal field conditions the figures would be extremely valuable. Nevertheless, they are useful in showing the approximate conditions.

The small special collections (type 2) are valuable because they show that *B. compsilurae* is present over the whole area.

THE ADULT

(*Chalcis*) *Brachymeria compsilurae* was described by Crawford (*6*) in 1911. The adult is similar to *B. intermedia* (fig. 1, *A*), although the markings of the hind legs and the malar carinae show differences, as illustrated in figure 1, *D* and *E*.

THE EGG

The egg (fig. 4, *B*) is of the usual form, but is unusual in being surrounded by a clear, hyaline membrane. The egg body averages

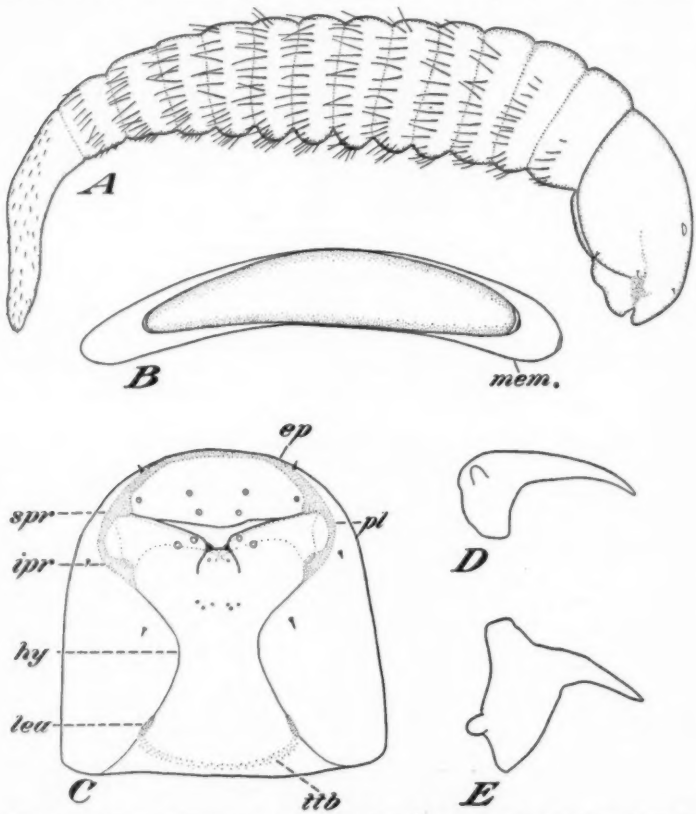

FIGURE 4.—*Brachymeria compsilurae: A*, First-instar larva (× 120). *B*, Egg, showing membrane, *mem* (× 55). *C*, Head of first-instar larva (× 275); *ep*, epistoma; *spr*, superior pleurostomal ramus; *pl*, pleurostoma; *ipr*, inferior pleurostomal ramus; *hy*, hypostoma; *lea*, lateral epicranial angle; *itb*, transverse tentorial bar. *D*, first-instar mandible (× 400). *E*, Second-instar mandible (× 500).

1.04 mm long and 0.23 mm wide. It is slightly curved, with rounded ends, being somewhat wider at the cephalic end. The chorion is smooth except for a slightly roughened area at the micropyle. The embryo is yellowish. The envelope is about the same shape and width as the egg body, but it is considerably longer. It is so delicate

that it collapses when the egg is dissected out of the host, but soon regains its shape if floated in water. When floated in normal saline solution, the membrane becomes slightly turgid. An average specimen measures 1.60 mm long and 0.23 mm wide, while some specimens as long as 2.00 mm have been noted. The cephalic end bears a slightly roughened area comparable to the micropyle of the egg body.

THE FIRST-INSTAR LARVA

The first-instar larva (fig. 4, *A*) differs from that of *Brachymeria intermedia* in having a well-developed tail. It closely resembles that of *B. fonscolombei*, belonging to Parker's group 5 (*20, fig. 104*).

The newly hatched larva is 1.21 mm long and 0.18 mm wide; its body form is shown in figure 4, *A*. The head is well differentiated, followed by 13 distinct segments, the last of which is prolonged into a tail. The tail is as long as 3 or 4 body segments and tapers posteriorly. Parker (*20, p. 270*) found that, contrary to the usual manner in larvae, the tail of *B. fonscolombei* probably results from a fusion of body segments 12 and 13, there being only 12 segments in his larva. *B. compsilurae*, on the contrary, has 12 distinct segments followed by the tail. Each of the body segments bears a transverse row of long delicate spines, as indicated in the figure. The spines on the tail are considerably shorter and broader than the others. No sensory setae were distinguished on the body segments.

The head is thimble shaped and lightly sclerotized. The antennae are inconspicuous rounded elevations. The mouth opening is on the ventral side at the apex. The mandibles (fig. 4, *D*) are 0.066 mm long. They are well sclerotized and yellowish at their tips. Viewed ventrally, the head (fig. 4, *C*) presents well-defined characters, although the sensoria are distinguished with difficulty and those on the labium have been seen only in living specimens. The weekly sclerotized hypopharyngeal bracon is not indicated in the figure. It is strongly depressed and weak at the center.

The tracheal system is composed of a pair of lateral longitudinal trunks united anteriorly in the first thoracic and posteriorly in the ninth abdominal segment. There are no open spiracles, but rudimentary spiracular branches occur in the second and third thoracic and the first seven abdominal segments. The dorsal tracheal branches arise from both the spiracular branches and the main longitudinal trunk. The ventral branches arise from the longitudinal trunk near the base of the spiracular branches. The head is supplied from branches arising in the first thoracic segment, and the tail receives long branches from the longitudinal trunks in the ninth abdominal segment.

The digestive, nervous, and circulatory systems are similar to those described for *Brachymeria intermedia*, with the following minor exceptions: The hind-intestine terminates on the ventral surface of the basal part of the tail, the salivary glands are somewhat less regularly serpentine and they terminate in the eighth abdominal segment, the dorsal malpighian tubes are not sinuous but straight, the anterior malpighian tubes extend forward to the first or second abdominal segment, and the ventral nerve cord extends back to the eighth abdominal segment, where the last fused ganglion gives rise to 3 pairs of nerve cords instead of 2.

THE SECOND-INSTAR LARVA

Second-instar larvae are from 1.58 mm long and 0.44 mm wide to 2.28 mm long and 0.75 mm wide. In its form this instar (fig. 5, *A*) is

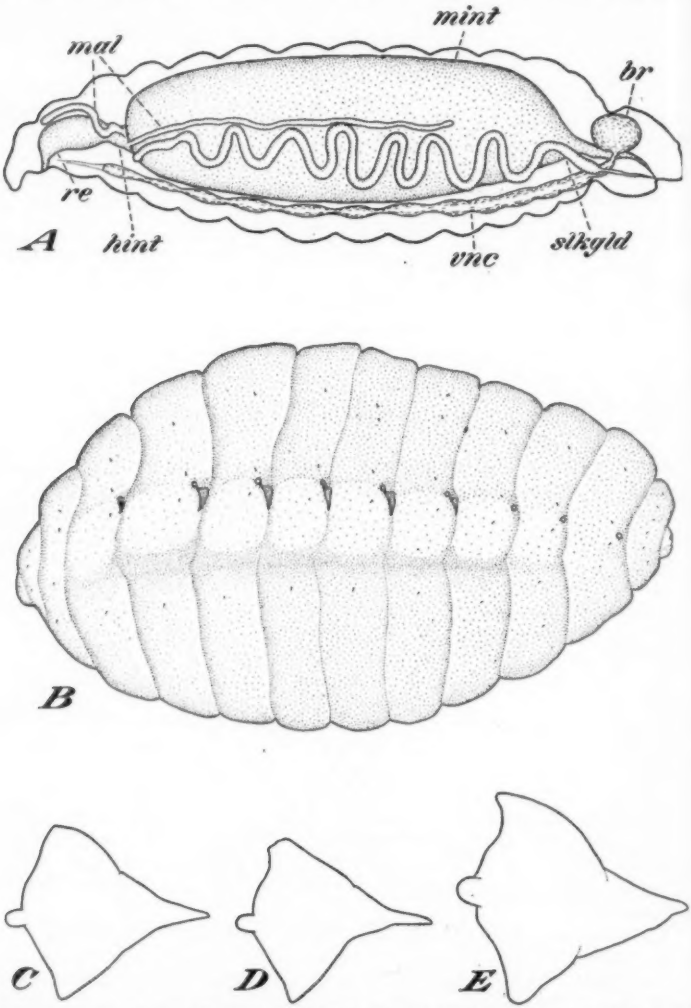

FIGURE 5.—*Brachymeria compsilurae*: *A*, Second-instar larva, internal anatomy (× 62); *br*, brain; *mint*, mid-intestine; *mal*, malpighian tubes; *re*, rectum; *hint*, hind-intestine; *vnc*, ventral nerve cord; *silkgld*, silk gland. *B*, Full-grown larva (× 10). *C*, Third-instar mandible (× 387). *D*, Fourth-instar mandible (× 234). *E*, Fifth-instar mandible (× 200).

quite different from the first instar. The body is much stouter and the tail, although still pointed, is much shorter and thicker. The cuticular armature is also entirely different in this instar. The spines are very short, and each segment bears several rows. The first

segment has 3 or 4 rows on the venter which extend about to the median line of the pleurum, but it has none on the dorsum. All the other segments have 3 or 4 rows on the venter which gradually disappear toward the median line and then increase until 2 or 3 rows of somewhat shorter spines are present on the dorsum. The last 3 abdominal segments have more spines on the dorsum than on the venter, and the tail is thickly covered on the dorsum but is bare on the venter. All the cuticular spines are pointed backwards. No sensory setae were distinguished on the body segments.

The head, although more heavily sclerotized, has the same characters as in the first instar. The antennae are much more prominent. The mandibles (fig. 4, *E*) are much broader at the base, but are actually shorter, being only 0.053 mm long.

The tracheal system, as in the first instar, has no open spiracles, but rudimentary spiracular branches may be distinguished in the second and third thoracic and first 7 abdominal segments.

THE THIRD-INSTAR LARVA

Third-instar larvae are from 2.73 mm long and 1.10 mm wide to 3.52 mm long and 1.33 mm wide. The body is stouter than in the second instar. The tail is still noticeable, being pointed, but it is very little longer than the other body segments. The cuticular armature is almost the same as in the second instar, but usually there are a few forward-pointed spines on the posterior ventral borders of the first 6 or 8 abdominal segments. In this instar sensory setae were distinguished on the body segments for the first time. Each segment except the last apparently has 3 pairs, 1 on the dorsum, 1 near the spiracles, and 1 half way between the spiracles and the venter. None was found on the last abdominal segment.

The head is much smaller, but otherwise exactly like that of the full-grown larva. The mandibles (fig. 5, *C*) are 0.086 mm long.

The tracheal system has 9 pairs of open spiracles, 1 pair on each of the second and third thoracic and on each of the first 7 abdominal segments. The mesothoracic spiracle is approximately 0.023 mm in diameter.

THE FOURTH-INSTAR LARVA

Fourth-instar larvae are from 4.42 mm long and 1.76 mm wide to 5.90 mm long and 2.64 mm wide. The body is well rounded, approaching the appearance of the full-grown larva. The cuticular armature has the same arrangement as before, although there is a slight increase in the number of rows of spines on each segment. The number and arrangement of the sensory setae is exactly the same as in the full-grown larva (fig. 5, *B*).

The head has the same characters as the full-grown larva. The mandibles (fig. 5, *D*) are about 0.12 mm long.

The tracheal system is like that of the third-instar larva. The mesothoracic spiracles are about 0.04 mm in diameter.

THE FIFTH-INSTAR LARVA

When reared from the large tachinid, *Sturmia scutellata*, the full-grown, or fifth-instar, larva (fig. 5, *B*) is from 5.7 mm long and 2.6 mm wide to 10.0 mm long and 5.0 mm wide, but when reared from *Comp-*

silura concinnata, which is a much smaller tachinid, the full-grown larva averages about 5.72 mm long and 2.82 mm wide. It is strikingly oval in shape and of a glistening yellowish-white color with distinct segmentation. The tail is simply a tiny terminal segment, somewhat pointed. There are no cuticular spines. The sensory setae are inconspicuous, the largest being only 0.033 mm long, but their position has been indicated in the drawing. Their number and position are the same as in the full-grown larva of *B. intermedia* (fig. 3, *A*). Little wedge-shaped, yellowish, sclerotized plates are conspicuous just below the spiracles of abdominal segments 2 to 7, inclusive. Parker (*20, pp. 298–299*) has also described such plates in *B. fonscolombei*. Their function is unknown. On freshly molted fifth-instar larvae these plates cannot be distinguished. They rapidly become yellowish, however.

The head is so much like that of *B. intermedia* that it will not be described or illustrated separately. The only apparent differences are as follows: The 2 pairs of sensory spines that lie above and laterad of the antennae in *B. intermedia* cannot be distinguished in *B. compsilurae;* the antennae of *B. intermedia* are simple, while in *B. compsilurae* they are almost invariably divided or two-segmented; finally, the mandibles of *B. intermedia* (fig. 3, *G*) are less robust than those of *B. compsilurae* (fig. 5, *E*). The mandibles of *B. compsilurae* are about 0.17 mm long and 0.15 mm wide.

The tracheal system is essentially the same as in the preceding instars, but the branches are much larger and more ramified.

The digestive system is practically the same as in the second instar (fig. 5, *A*), although the mid-intestine is now a large oval sac. In the full-grown larva the salivary-gland tubes extend only to the sixth abdominal segment. Parker's figure (*20, fig. 251*) shows the digestive system of *B. fonscolombei* to be very similar, although the hind-intestine in *B. compsilurae* is much larger, occupying a large part of the ninth abdominal segment.

The nervous system is of the usual type, consisting of the brain, subesophageal ganglia, and nerve cord connecting 11 pairs of ganglia. Each ganglion gives off a long nerve fiber, and the terminal pair probably represents the fusion of 3 pairs, because 3 pairs of nerve fibers arise from it. The terminal ganglion is in the sixth abdominal segment.

The histoblasts and the fat body are conspicuous in this instar, occupying the same relative positions as in the full-grown larva of *B. intermedia*.

THE PREPUPA

If a second generation of *B. compsilurae* develops during the season, the fifth-instar larva voids its meconium almost immediately after becoming full fed, and the prepupa may be clearly distinguished, as in *B. intermedia*. If another generation of *B. compsilurae* does not develop during the season, the winter is passed as a full-grown larva, and the meconium is voided in the spring.

THE PUPA

The pupa is of the usual hymenopterous type, presenting no great differences from that of *B. intermedia*.

SEASONAL HISTORY

Brachymeria compilsurae overwinters as a full-grown larva within the puparium of its host, and its seasonal development depends to a large extent upon the host which it parasitizes. If the adult attacks a single-generation tachinid, such as *Sturmia scutellata*, the resulting progeny remain as full-grown larvae until the following year, thus completing but one generation. But if the adult attacks a multibrooded tachinid, such as *Compsilura concinnata*, 1, 2, or even 3 generations may develop during the season. These conditions can be described best by comparing the life history of the parasite upon the two different types of tachinid host species, but it must be borne in mind that in nature the parasite may readily shift from one to the other.

When *B. compsilurae* parasitizes *S. scutellata*, adult emergence begins about the middle of June and continues until about the middle of July. *P. dispar* pupae are already present in the field at this time, and *Sturmia* maggots may be attacked from about the middle of July until the middle of August. *B. compsilurae* larvae rapidly become full grown, and hibernation takes place in this stage. The meconium is cast the next spring, and prepupal and pupal transformations follow in short order.

When *B. compsilurae* parasitizes *Compsilura concinnata*, adult emergence begins about June 1 and continues until about June 20. The first hosts attacked in the field are probably *C. concinnata* developing in larvae of *Stilpnotia salicis* or *Porthetria dispar*, which become available about June 20. Second-generation adults of *Brachymeria* begin issuing about July 21 and continue to come out until the first of August. In the laboratory these second-generation adults attacked *C. concinnata* developing in *Hyphantria cunea* Dru. and *Euchaetias egle* Dru. between July 29 and August 12. Third-generation adults appeared between August 28 and September 8. Females of this generation attacked *C. concinnata* developing in *E. egle* between September 6 and 13. All the full-grown larvae of this generation hibernated.

TABLE 3.—*Summer-issuing and hibernating Brachymeria compsilurae from Compsilura concinnata attacked on different dates in 1933*

Generation of adult parasite that oviposited	Date of attack	Summer-issuing *Brachymeria*	Hibernating *Brachymeria*
		Number	*Number*
First:			
Adult issued from *Sturmia scutellata*	June 24	9	1
	June 25	19	
	June 26	29	10
Adult issued from *Compsilura concinnata*	do	6	17
	June 27	42	0
Second	July 29	6	0
	Aug. 5	3	10
	Sept. 6	0	17
	Sept. 7	0	9
Third	Aug. 11	0	5
	Aug. 13	0	2

This summary of the development of *B. compsilurae* in *C. concinnata* does not take into consideration the number of larvae of each generation which hibernate. This phase in the life history is confusing, for

there does not seem to be any rule governing the diapause. In 1932 the number of larvae entering hibernation seemed to increase as the season advanced. From *C. concinnata* attacked by first-generation adults from June 29 to July 1, 49 *Brachymeria* were reared; 39 adults issued the same season, while 10 larvae, or about 20 percent, hibernated. Out of 95 *Brachymeria* reared as progeny of second-generation adults which attacked *C. concinnata* from August 6 to 18, 20 adults issued, and 75 larvae, or about 80 percent, hibernated. In 1933, however, there seemed to be no definite hibernation tendency. In one lot attacked on June 26 the majority of *B. compsilurae* issued the same season, while in other lots attacked on the same date the majority hibernated. The results are shown in table 3.

These records show not only the extreme variability in hibernation tendency in the first two generations reared from *Compsilura*, but also that, whether the first-generation adults issue from *Sturmia* or from *Compsilura*, they readily attack *Compsilura* and their progeny exhibit the same tendencies regarding summer issuance.

HABITS OF THE ADULT

When *Brachymeria compsilurae* is ready to emerge, it first cuts a small hole at about the third segment of the host puparium. It then cuts around the puparium, roughly following the line of cleavage between the cap and the rest of the puparium, by placing one mandible inside and one outside and chipping away at the hard shell. When the cut extends about four-fifths of the way around, the parasite pushes the cap off with its head. The adults, like those of *B. intermedia*, appear very clumsy in confinement, but they are graceful fliers. Both sexes thrive in confinement when held in cages like those used for *B. intermedia*. Ten females that issued on June 15, and were used almost daily in reproduction work, lived an average of 40 days, with a minimum of 27 and a maximum of 57 days. Twenty males issuing on June 13 lived an average of 49 days, with a minimum of 17 and a maximum of 81 days. If the insects are kept continuously in a cool, dark place, they will, of course, live much longer. One male held in this manner lived 121 days and one female lived 140 days.

Brachymeria compsilurae adults mate readily in confinement, mating proceeds almost exactly as it does with *B. intermedia*, and the same optimum conditions hold for both species. Pairs remained in coitu between 10 and 20 seconds, with an average of 15½ seconds, in 12 recorded instances. The age of the female seems to have little influence on fertilization. Three females that were 20 days old and had already laid a number of unfertilized eggs mated readily. They subsequently oviposited again, and both sexes were represented in their progeny, indicating that they had been fertilized.

Some *B. compsilurae* females have been known to oviposit within a day after emergence, but oviposition does not proceed readily until they are 2 or 3 days old. Interest is shown in any lepidopterous larva or pupa that is dead or motionless, but seldom is much attention paid to a primary host that does not contain a tachinid maggot. Living larvae or pupae are avoided. After the female has chosen her victim, she mounts it and walks over it slowly. Now and then she stops, elevates her body, unsheaths her ovipositor, and slowly pushes

it into the caterpillar or pupa. If she encounters a tachinid maggot, the female oviposits immediately. If, however, she finds none, she moves forward, withdrawing her ovipositor. Usually a female inserts her ovipositor in a caterpillar or pupa several times and is often occupied with it for 10 minutes or longer. If other females are present, they often strike at one another with their hind legs, but these battles are seldom serious enough under laboratory conditions to interfere with the more imperative desire to oviposit, and often 2 or 3 females will oviposit in 1 maggot at the same time.

Evidently a tachinid maggot itself is not enough to induce oviposition, for free maggots are avoided. The dead or dying primary host must be present, and there is evidence that the parasites are guided somewhat by the sense of smell. Several times, when an ovipositing female caused a maggot to writhe with especial violence, a drop or two of the brown liquid commonly surrounding an almost full-fed tachinid maggot oozed out on the vial or box. Other females would repeatedly try to insert their ovipositors in these drops of liquid. As soon as they were dry, however, no further attention was paid them.

The reproductive capacity of the females was not determined satisfactorily. Ten females were isolated and kept constantly supplied with host material, but they did not live long. Six of them laid from 38 to 48 eggs each, with an average of 42, but upon dissection large numbers of eggs were still present in the ovarioles. No more than 12 eggs were laid in a single day, but this number wa frequently obtained. This is probably the total daily capacity, for each ovary has 6 ovarioles, and the eggs are apparently too large to permit development of more than 1 at a time.

Unmated *B. compsilurae* females oviposit readily, and only males are produced by parthenogenesis. No satisfactory records have been kept on the proportion of the two sexes issuing from field-collected material, but there are indications that the sexes are about equal. In 1932 a lot of 70 individuals comprised 29 males and 41 females, and in 1933 a lot of 100 individuals consisted of 57 males and 43 females.

DEVELOPMENT OF IMMATURE STAGES

The egg of *Brachymeria compsilurae* remains about where it is laid, in the body cavity of the host maggot. Hatching takes place in about 48 hours, and the young larva starts feeding immediately on the blood and lymph of the host. The parasite larva is a typical internal feeder, having a long tail and a closed tracheal system. It closely resembles the larva of *B. fonscolombei*, which was figured by Parker (*20, figs. 103–104*). No more than one *B. compsilurae* larva ever completes development in a host, even when more than one egg is laid. As with *B. intermedia*, all the dead larvae observed have borne marks that might have been made by the mandibles of another larva. The young larva apparently does not develop beyond the first instar until the host metamorphosis from larva to pupa takes place. It then apparently feeds indiscriminately, for it soon eats out a bubblelike area in the host's body contents, and by the time it is in the second instar it can usually be found in this space. The larva invariably consumes the entire body contents of the host, which vary greatly in size, and there is therefore considerable varia-

tion in the size of the adult parasites. When feeding is completed, the larva may void its meconium and transform to a pupa, or it may remain as a larva in the host puparium all winter, voiding its meconium in the spring. When feeding is completed, the head end of the parasite is always directed toward the cephalic end of the puparium.

The time required for development from egg to adult depends somewhat on the condition of the host larva when it is attacked. If the tachinid larva is full grown and issues from its host within 48 hours after the *Brachymeria* egg is laid, the hyperparasite develops rapidly. If the tachinid larva does not issue and form its puparium for several days, growth of the hyperparasite larva is retarded. It apparently never develops beyond the first instar until the host forms its puparium. A first-instar parasite larva has been found in a tachinid maggot 6 days after egg deposition. If the maggot had formed its puparium on the first or second day, the larva would probably have been in the third instar. Temperature also affects the rate of development. Under laboratory conditions host larvae attacked during June, July, and August showed no great variations, however. From 23 to 28 days were required for the development of males and from 25 to 31 days for that of females. Larval development was observed during July by dissecting 57 host puparia that were formed 2 days after the maggots were attacked. These dissections indicated that 2 days were spent as an egg, about 2 days as a first-instar larva, 1 day in each of the second and third larval instars, 2 days in the fourth instar, 3 days in the fifth instar, 2 days as a prepupa, and 12 days as a pupa, making a total of approximately 25 days.

FACTORS LIMITING THE EFFECTIVENESS OF THIS PARASITE

Brachymeria compsilurae is a species that has taken advantage of a new supply of food and has increased enormously in numbers. Its principal host species, *Compsilura concinnata* and *Sturmia scutellata*, have been established in North America so long, however, that, if the secondary parasite were capable of overtaking them, it would probably have done so by this time. Just what has limited its increase is problematical. The only known factor curtailing it is another secondary parasite, *Monodontomerus aereus* Walk., which undoubtedly parasitizes *B. compsilurae* when it is a parasite of *C. concinnata* in *Nygmia phaeorrhoea*. The number that are thus accidentally attacked must be very small, however. Possibly the wide range of hosts in which *C. concinnata* develops protects this species somewhat, but there seems to be nothing to protect *S. scutellata*. The fact remains that, in spite of serious losses through *B. compsilurae*, both these beneficial tachinids have continued to maintain themselves.

COMPARISON OF THE TWO SPECIES

The adults of *Brachymeria intermedia* and *B. compsilurae* have been found to be very similar. Their habits of mating are almost identical, their methods of oviposition are much the same although the stage and condition of the host oviposited in are different, and their seasonal histories are similar, with each producing several generations. But here the similarity ends. The two species present entirely different

host relations, their hibernation habit differs, and their immature stages are radically different.

The egg of *B. intermedia* is of the conventional type, whereas that of *B. compsilurae* is unusual in that it has an enveloping membrane. No other hymenopterous egg with such a membrane has been figured, although the writer has found one around the egg of *Cremastus interruptor* Grav., a parasite of *Rhyacionia buoliana* Schiff. The first-instar larva of *B. intermedia* closely resembles external feeding larvae, but that of *B. compsilurae* is typical of the caudate form of internal feeding chalcidoid larvae. The advanced instars of *B. intermedia* do not differ greatly from the first instar, but in the case of *B. compsilurae* the appearance changes considerably owing to the gradual loss of the tail, and the full-grown larva bears 6 sclerotic plates below the spiracles of abdominal segments 2 to 7, inclusive. The head of the full-grown larva, however, is practically the same in both species, and their internal anatomy is very similar.

SUMMARY

Brachymeria intermedia (Nees) and *B. compsilurae* (Cwfd.) are, respectively, primary and secondary parasites of the gypsy moth (*Porthetria dispar* L.).

Brachymeria intermedia is a polyphagous European species which is of primary importance as a parasite of *P. dispar* pupae in Sicily, Algeria, and Morocco. It is a minor factor in the more northern latitudes of central Europe, probably requiring a warmer climate to become effective. Several unsuccessful attempts have been made to establish it in New England. This species overwinters as an adult, passing through 2, and possibly 3, generations in a season. *P. dispar* is probably the first host species to be attacked in central Europe after the adults leave hibernation. The adults thrive and mate readily in confinement. They oviposit in the host pupa, and development from egg to adult requires from 18 days in August to 62 days for eggs laid in September. The egg of *B. intermedia* is of the conventional type. There are five larval instars. The first-instar larva closely resembles typical external feeding chalcidoid larvae, and the advanced larval instars do not differ greatly from the first instar.

Brachymeria compsilurae is a species occurring in North America which, so far as is known, acts solely as a parasite of tachinid flies. It has been reared from many species of Tachinidae, and is particularly destructive to *Compsilura concinnata* and *Sturmia scutellata*, which are European parasites successfully established in New England against the gypsy moth. *B. compsilurae* overwinters as a full-grown larva within its host puparium. It develops only 1 generation in single-generation tachinids, but passes through 2 or 3 generations in multi-brooded host species. The adults thrive and mate readily in confinement. They oviposit through the primary lepidopterous host pupa or larva, locating the tachinid maggots probably through a sense of smell. Development from egg to adult requires from 23 to 28 days in males and from 25 to 31 days in females. The egg is unusual in that a clear hyaline membrane encloses an egg body of the conventional type. There are five larval instars. The first-instar larva is typical of the caudate form of internal feeding chalcidoid larvae. The advanced instars change considerably owing to the

gradual loss of the tail. The full-grown larva is unusual in having 6 sclerotic plates below the spiracles of abdominal segments 2 to 7, inclusive.

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TRICHOSPORIUM SYMBIOTICUM, N. SP., A WOOD-STAINING FUNGUS ASSOCIATED WITH SCOLYTUS VENTRALIS[1]

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INTRODUCTION

During the past several years an engraver beetle (*Scolytus ventralis* Lec.) has caused the death of many white firs (*Abies concolor* Lindl. and Gord.) throughout the Sierra Nevadas of California. The galleries are confined to the cambial region, and the eventual death of the infested tree is the result of girdling.

A brown discoloration has been known to be commonly associated with *Scolytus ventralis* tunnels, but it was not until 1930 that the cause of the stain was discovered. In that year an investigation was started by the Division of Forest Insects, Bureau of Entomology and Plant Quarantine, United States Department of Agriculture, on the insects infesting white firs, and Struble[3] isolated a fungus from a number of the stained areas. Inoculations with the isolated organism produced a similar brown discoloration in the wood and inner bark of uninfested trees.

Subsequent to this work and at the invitation of the Division of Forest Insects, the writer carried on additional studies of the fungus in an attempt to determine its role in the development of beetle broods. The results of these studies and a description of the fungus are given in the present paper. Special effort has been made to determine the pathogenicity of the fungus to white fir and the manner in which it is transmitted from tree to tree.

REVIEW OF LITERATURE

In 1931 Rumbold (*13*)[4] reviewed the literature relating to bark beetles and blue-staining fungi. In her own investigations she established the fact that blue stains are frequently associated with species of *Ips* and *Dendroctonus*. Grosmann (*7*) studied Ipids and concluded that the different associated fungi have the same requirements for living as the beetles but that the insects are important carriers of blue stain and related organisms. Investigators have shown that bark beetles frequently act as direct carriers of infection.

Ceratostomella (*Graphium*) *ulmi* (Schwarz) Buisman, which causes the serious Dutch elm disease, seems to be the only wood-staining fungus so far reported to be associated with *Scolytus* beetles. Wollenweber

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[3] STRUBLE, G. R. THE FIR ENGRAVER BEETLE AND ASSOCIATED INSECTS IN WHITE FIR. PRELIMINARY REPORT. U. S. Dept. Agr., Bur. Ent. 1931. (Unpublished.)

[4] Reference is made by number (italic) to Literature Cited, p. 538.

and Stapp (*14*) suggested that the frequent occurrence of *G. ulmi* in connection with *Scolytus* galleries may indicate that these beetles aid in spreading the disease, although actual proof was not obtained. Betrem and collaborators (*3*) showed, however, by isolations that *S. scolytus* Fab. adults actually carry the spores of *G. ulmi* both internally and externally. Since the spread of the Dutch elm disease to the United States, Beattie (*1*) has reported that May and Fowler isolated *G. ulmi* from imported elm logs containing *S. scolytus* broods. This interception was later supplemented by others and strongly suggests that these beetles may have played an important part in introducing the disease from abroad.

In some instances a symbiotic relationship between fungi and beetles has been indicated. Hubbard (*9*) in his study of ambrosia beetles showed that an interdependence does exist. For bark beetles true symbiosis is unusual.

MATERIALS AND METHODS

In order to secure an abundant supply of recently infested white fir material and newly emerged beetles, field laboratories were established in close proximity to the forest entomology camps where studies of *Scolytus ventralis* were at the time being pursued. The camps were situated at different localities, at elevations of 3,000 to 5,000 feet. Occasional material collected from other areas was also utilized in the course of the study.

The investigation so far has been confined to white fir, although *Scolytus ventralis* also infests other species, such as red fir (*Abies magnifica* Murr.), in this same section. Since the latter species occurs at higher elevations, the beetle emergence period is considerably shorter and infestations are less favorable for continued study.

Material for a close study of the fungus that causes the stain was obtained from freshly infested firs. Individually stained areas of xylem and inner bark were prepared for culturing by cutting away surface contamination with a flamed scalpel, thereby exposing fresh stain. Slivers were removed aseptically and planted on malt agar (2.5 percent malt extract to 2.5 percent agar) in Petri dishes. Isolations were later transferred to test-tube slants.

THE STAINING FUNGUS

ISOLATION

Stained material was cultured from 100 different galleries during the course of the study. A summary of the isolation results is presented in table 1.

TABLE 1.—*Isolations from Scolytus ventralis galleries in Abies concolor*

Material	Location of tree	Total galleries cultured	Cultures from galleries showing—		
			Causal organism	Other fungi	No organism
		Number	*Number*	*Number*	*Number*
Recent stain in inner bark	Stanislaus National Forest	16	14		2
Recent stain in xylem	do	10	8	2	
1-year-old stain in xylem	do	11	6	3	2
Recent stain in inner bark	Sequoia National Forest	8	8		
Recent stain in xylem	do	32	26	4	2
Do	Sierra National Forest	13	10	2	1
Recent beetle entrance holes	do	10	5	5	
Total		100	77	16	7

From a total of 100 isolations attempted, 77 produced cultures of the causal organism, 16 contained other fungi, and 7 were negative. The fungi other than the causal organism did not occur consistently. A few of the more unusual types were reduced to pure cultures for use in future tests to determine their staining possibilities.

In a few cases conidiophores of the fungus were observed as delicate, whitish hyphae in vacated *Scolytus ventralis* galleries. Because of their fragile character it is difficult to detect such formations regularly, and cultures were needed for verification.

Unlike the common blue stains in trees, the brown discoloration does not penetrate deeply into the sapwood and is confined to the annual ring in which the galleries are made.

A comparison of the fungus with Struble's isolations showed that the strains were identical in cultural as well as in microscopic features.

IDENTITY OF THE FUNGUS

There is general agreement that the fungus belongs in the Dematiaceae and to the genus *Trichosporium* Fr. No description has been found in the literature which can be applied to the organism referred to in this paper. It therefore appears necessary to designate the fungus as a new species.

TECHNICAL DESCRIPTION

Trichosporium symbioticum, n. sp.

Hyphis septatis, pallidis vel fuscis brunneis, intercellularibus, mediocribus 3.0μ diam.; conidiophoris ramosis, septatis, hyalinis, 1μ–1.5μ crassitudine; conidiis hyalinis, subglobosis, sessilibus, apice insertis, capitulatis et subterminalibus pleuracrogenis, 1.8μ–2.4μ diam.

Hyphae septate, colorless to brown, intercellular, averaging about 3μ in diameter. Conidiophores septate, colorless, 1μ–1.5μ in diameter, and bear clusters of spores inserted on the apices or occasionally subterminally of the main axis or on secondary or tertiary branches. Spores attached at the tips, hyaline, subglobose, 1.8μ–2.4μ in diameter. Associated with *Scolytus ventralis* Lec. galleries, causing a brown stain in the cambium and adjacent xylem and phloem of *Abies concolor* Londl. and Gord. in Californa.

In malt-agar cultures, submerged mycelium eventually fuscous brown, averaging 6μ in diameter, conidiophores colorless, clustered, erect, septate, 1.5μ–2μ thick, spores variable in size, 1.5μ–4μ in diameter.

On Abietineae (*Abies concolor* Lindl. and Gord.), California.

Type locality.—Strawberry, Stanislaus National Forest. Stan. W–201 wood and bark, herbarium, Division of Forest Pathology, San Francisco, Calif. Parts of type also deposited in mycological collections, Division of Mycology and Disease Survey, Bureau of Plant Industry, United States Department of Agriculture. Test-tube and plate cultures deposited with each collection.

The two distinguishing features that segregate this species from most other described species of *Trichosporium* are the colorless spores and their minute size. Descriptions of species that have colorless spores were found inapplicable, mainly because of their considerably larger spore size or in some cases because other characters as well did not agree, such as the color of the hyphae and the shape of the spores. A few of the descriptions given in the literature were not adequate for accurate comparison.

CULTURAL CHARACTERISTICS

Pure cultures of the fungus were grown on malt, potato-dextrose, corn-meal, starch, and modified Czapek's [5] agar. On malt agar

[5] KH_2PO_4 was used in place of K_2HPO_4 since an acid medium is more satisfactory for growing wood-inhabiting fungi.

which was the most favorable medium used, two kinds of mycelium were produced, (1) a white flocculent aerial mycelium, bearing conidiophores and spores, and (2) dark submerged hyphae, varying from cinnamon drab to fuscous brown in color. The submerged hyphae do not show noticeable coloration until the culture is 10 to 15 days old. The older the culture the darker the submerged mycelium becomes. On other agars the mycelium shows different degrees of coloration, all less distinct than that on malt agar, and no coloration on the Czapek's agar. Figure 1 shows the characteristic development of the mycelium under cultural conditions.

FIGURE 1.—*Trichosporium symbioticum* on malt agar, showing white flocculent air mycelium and dark submerged hyphae. Natural size.

MORPHOLOGY

In malt agar (pH 5.5) the dark-brown submerged mycelium is plainly septate and in old cultures the hyphae may obtain a maximum width of 14μ, with an average of 6μ. The whitish aerial hyphae are more delicate, ranging from 1.5μ to 2μ in width, and are also septate. Conidia are distinct from the conidiophores and occur in capitate clusters at their tips but occasionally subterminally as well. The spores are attached by the tips and are permanently hyaline, subglobose to ovoid in shape, and 1.5μ to 4μ in diameter. The conidiophores often divide into two or more branches, each of which may bear a capitate group of spores on the apices as illustrated in figure 2.

Microtome sections of infected wood, stained by the Cartwright (*6*) and Hubert (*10*) methods, when examined microscopically showed the presence of *Trichosporium symbioticum* hyphae within the tracheids,

and occasionally conidiophore and spore formations were also detected. Figure 3 is a photomicrograph showing *T. symbioticum* hyphae and spores within the tracheids of *Abies concolor* wood. The hyphae effect an entrance into the tracheids through the bordered pits and not directly through the cell walls. Hyphae also enter the medullary ray cells through the pits but are not as typically congregated here as is frequently the case with other wood-staining organisms such as *Ceratostomella* spp. Hyphae have been seen in the phloem parenchyma, but only indistinctly.

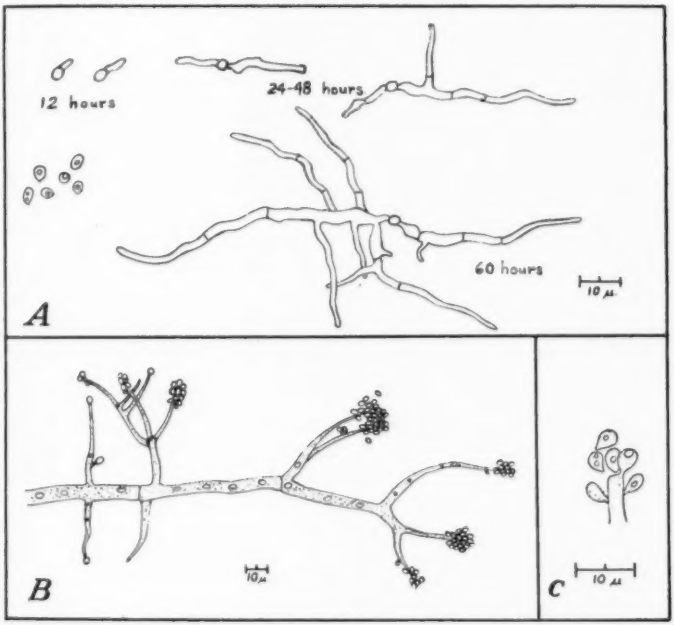

FIGURE 2.—*Trichosporium symbioticum* on malt agar: *A*, Spore germination and mycelial growth at 22° C.; *B*, typical aerial mycelium and conidiophores; *C*, enlarged tip of a conidiophore, showing manner of spore attachment.

In the tracheids of *Abies concolor* wood the maximum width of mycelium observed is approximately 8μ, averaging about 3μ. The spores produced in the tracheids are subglobose and vary from 1.8μ to 2.4μ in diameter. The sizes of the spores and hyphae do not differ as much within the tracheids as when the organism is grown in culture media.

OCCURRENCE OF STAIN IN GALLERIES OF SCOLYTUS VENTRALIS

To determine the frequency of stain occurrence in relation to *Scolytus ventralis* galleries, five infested trees were examined after they had been felled and the bark had been removed. These trees ranged from 8 to 30 inches in diameter. In all, 532 galleries were inspected macroscopically in consecutive order, and the brown discoloration was plainly evident in every case.

Special attention was given to evidences of overcome and unsuccessful beetle attacks, generally characterized by isolated galleries, to determine whether the brown discoloration was noticeable, thereby indicating the presence of *Trichosporium symbioticum*. In no instance was the coloration found to be entirely lacking, although the areas stained in unsuccessful attacks appeared to be less extensive than in successful infestations.

In trees where the beetle attacks are but few or have been unsuccessful, the stain is soon overgrown by newly formed xylem so that it becomes buried under successive layers of annual growth. Years later, when such trees are felled and bucked, the stained areas may become evident on the cross cuts. The date of the attacks may be readily established by counting the number of rings that have been formed over the stain (fig. 4).

FIGURE 3.—Hyphae and spores of *Trichosporium symbioticum* within tracheids of *Abies concolor* wood. × 450

The trap trees [6] used by the entomologists to attract *Scolytus ventralis* provided another means of studying the frequency of the occurrence of the fungus with individual egg galleries. Several weeks after the attacks were made the bark was removed from seven different trap trees and 999 galleries were examined successively. Stain was plainly evident in all but 28, and these had been formed very recently. The number of trap-tree galleries inspected plus the number of galleries found in the infested firs makes a total of over 1,500 attacks examined. The stain was unquestionably present in all but 2 percent of the galleries, and the recent origin of these may explain its visual absence, since cultural isolations have already shown that the fungus was probably present in these doubtful cases.

At the time of the examination of the trap-tree attacks, measurements were made of the extent of the stain. Estimates of the approximate age of the egg galleries were based on their length. It was found that the discoloration spread longitudinally at an average rate of approximately 3 mm a day. It was possible to follow the rate at

[6] In this investigation a trap tree consisted of a purposely felled, living white fir that was left unlopped on the ground. Unlopped trees are especially attractive to *Scolytus ventralis*, and by using this method forest entomologists secured abundant infestations at will.

which the stain spread for about 1 month, but after that time the discoloration of adjacent galleries ran together (fig. 5). The measurements indicated that individual trap trees show considerable variation in the rate at which the stain spread from the galleries.

The beetles extend their mines as the eggs are laid, and the stain is therefore first noticeable in the older portions of the galleries. Before any of the eggs hatch into larvae, however, the brown discoloration spreads longitudinally from 30 to 50 mm on both sides of the egg gallery. With this start, the stain keeps well in advance of the fastest working larvae. The writer has never found larval mines that have extended into unstained areas.

FIGURE 4.—Section of *Abies concolor* tree heavily mined with *Scolytus ventralis* galleries. Dates indicate year of attack. Notice callus formations surrounding the overcome and unsuccessful attacks. Extent of stain associated with the 1931 attacks was outlined by the writer. Photographed by George R. Struble; approximately one-fifth actual size.

It appears from these examinations that when *Scolytus ventralis* attacks white fir a brown stain is regularly associated with the galleries of this beetle. Discoloration of the same sort has never been found except in connection with beetle infestations.

THE BEETLES AS CARRIERS OF THE STAINING FUNGUS

ISOLATIONS FROM LIVING BEETLES

Infested logs placed in the Bureau of Entomology and Plant Quarantine rearing cages provided a ready supply of beetles. The adults emerged into small glass jars on the front of the cages, and 100 beetles were collected in this manner. Each insect was placed in a 50-mm Petri dish containing lukewarm malt agar, where they swam about until the agar solidified. The beetles were then removed with sterile forceps and the plates were incubated. Microscopic examinations of the plates were made periodically.

A number of different fungi were found growing in the plates, but 90 percent produced cultures of *Trichosporium symbioticum*. The most common contaminants were *Penicillium*, *Aspergillus*, and *Mucor* spp., none of which occurred consistently. In a few instances the plates contained practically pure cultures of *T. symbioticum*.

The beetles in the above investigation were not collected singly, and there was a possibility of mutual contamination. To obviate this objection 25 additional beetles were removed from the bark of infested

white fir before they emerged, and were placed in separate sterile test tubes preparatory to cultural proceedings. Later they were removed from the test tubes into lukewarm agar and allowed to swim about as previously described.

These beetles all proved to be carriers of *Trichosporium symbioticum*. It may be assumed, therefore, that *Scolytus ventralis* commonly carries the staining fungus and in this way introduces it into the egg galleries. It appears that an occasional beetle that may emerge free of the fungus is likely to become a carrier afterward through contact with other beetles.

FIGURE 5.—Stain in the wood of an *Abies concolor* tree attacked by *Scolytus ventralis*. The stain is shown well in advance of the longest larval galleries, and in several cases the discoloration has spread from one colony to another, forming extensive areas. Photographed by J. M. Miller. Approximately one-fourth actual size.

ISOLATIONS FROM ALIMENTARY TRACTS

To determine whether the beetles carried *Trichosporium symbioticum* internally or externally, 50 *Scolytus ventralis* alimentary tracts were cultured by means of the following technic: Before the beetles were dissected they were sterilized according to a method used by Beckwith and Rose (*2*), who studied the intestinal flora of termites. The living beetles were placed in a U. S. P. tincture of iodine solution for 20 to 30 seconds. They were then washed in two changes of physiological saline solution and finally in two changes of sterile water. The beetles were dissected under sterile conditions by Struble. Each alimentary tract was plated immediately on malt agar by the writer. The plates were examined regularly during incubation.

Trichosporium symbioticum developed from only 4 of the 50 alimentary tracts. The small number of positive isolations indicates that the fungus is not commonly carried internally.

PATHOGENICITY TESTS

As a test of the pathogenicity of the isolated fungus, Struble [7] drilled a number of white fir trunks with a 3/32-inch bit to simulate the beetle galleries, and inoculated through these openings. The writer inoculated seven trees in a similar manner, mainly to determine the

[7] STRUBLE, G. R. See footnote 3.

rate at which the stain spread. The surface of the bark was sterilized with 70-percent alcohol and the drillings were made horizontally in an ascending spiral to avoid the effect of mechanical girdling. The inoculum, consisting of *Trichosporium symbioticum* in bits of malt agar, was inserted into the drill holes with a sterile needle. Check insertions of sterile agar were alternated with the inoculations in the same trees. Both the inoculations and checks were left undisturbed for 3 to 8 weeks. Then the bark was cut away to expose the stain and in some cases the trees were felled and the bark entirely stripped from the trunks. This revealed the presence of stain very clearly (fig. 6).

FIGURE 6.—Section of *Abies concolor* trunk, inoculated by the drill method, from which the bark has been removed. On the left the checks show the absence of stain (indicated by check marks). On the right are two inoculations showing the spread of the stain in the sapwood (after 4 weeks). Approximately one-half actual size.

Measurements from a total of 145 inoculations showed that the stain spread only approximately one-third as rapidly as the discoloration associated with the beetle galleries, the daily spread averaging 1 mm.

All the checks except 5 in 1 tree remained free of discoloration. The trunk of this particular tree was enclosed with a wire screen after inoculation, and a number of *Scolytus ventralis* adults were introduced later into this cage by the entomologists, to determine whether the beetles preferred stained or unstained areas in which to establish their egg galleries. The experiment failed to settle the question, possibly because of the presence of excessive balsam,[8] which had exuded from the drill wounds and which apparently restricted the beetles from making extensive explorations. Since both the checks and the inoculations were left open, it is possible, however, that exploring beetles did introduce the fungus into the five checks.

Reisolations were taken from four of the inoculated trees and reinoculated into other unstained white fir trees. Subsequent examinations revealed the presence of the brown discoloration in all reinoculations.

[8] Preliminary tests by members of the Division of Forest Insects, Bureau of Entomology and Plant Quarantine, have since shown that white fir balsam is actually very toxic to *S. ventralis* beetles.

Several other organisms, obtained during isolation studies, were also inoculated into white fir trunks but gave negative results.

CORK-BORER INOCULATIONS

To determine whether *Trichosporium symbioticum* could kill white fir trees without the aid of the beetle galleries, it was necessary to devise a method of inoculation in which the inoculum could be placed in the cambial region in such a manner that the stain would naturally spread to form a solid band around the tree trunk. To meet this requirement and to reduce the effect of mechanical wounding to a minimum, a cork-borer method of inoculation was employed (*15*).

FIGURE 7.—*Abies concolor* tree 10 months after inoculation with *Trichosporium symbioticum* by the cork borer method. Balsam has started to flow from the base of the girdle, which was produced by the coalescence of the stain. This is tree 7 in table 2. One-third actual size.

Twenty white firs growing on the same site were selected, 10 to be inoculated and 10 to be used as checks. Considerable care was exercised in these selections to obtain check trees that were as nearly as possible duplicates of the trees inoculated. Before the inoculations were made, the portion of the stem to be inoculated was carefully washed with 70-percent alcohol.

The method consisted of using a no. 3 cork borer to cut out a series of bark disks extending entirely around the tree trunk. From one-half to 1 inch of bark was left between borings, to obviate mechanical girdling. The borer was forced through the bark down to the xylem and carefully withdrawn containing the bark disk in the barrel. The inoculum, consisting of *Trichosporium symbioticum* in malt agar, was deposited in the hole with a sterile needle, and the disk was immediately replaced by forcing it from the barrel directly into place with a plunger.

After the completion of a ring of borings, a strip of waterproof adhesive tape was placed over the disks and around the tree trunk. This held each disk in position and prevented as far as possible the detrimental effect of drying out.

Since the fungus, as previously indicated by the stain spread, has only a limited lateral growth, it was necessary to arrange the inoculations in more than one ring. These were made about 2 to 3 inches apart, with the borings of the lower ring alternating with those of the

ring directly above. In this way the uninoculated areas between the borings would be more certainly invaded by the fungus hyphae as they extended longitudinally.

The checks were treated in the same manner as the trees inoculated, except that sterile malt agar was used instead of the inoculum.

The results secured from the cork-borer inoculations are presented in table 2, along with other essential data. The condition of the trees was judged largely on the general appearance of the crowns. Final examinations were made 16 months after the beginning of the tests. Examinations of the inoculated trees were made by peeling off the bark from the inoculated portions.

Eight months after the beginning of the tests the bark adjacent to the inoculated areas was much cracked and there was a considerable flow of balsam. On several of the trees definite cankers had formed and callus formation had started. All of the check trees at the time appeared normal, and only a very slight superficial cracking of the bark could be detected, with no external balsam flow. By midsummer of the year following the initiation of these tests, some of the inoculated trees had failed to produce new needles and a few dead branches could be seen in the crowns. The infected trees all showed pronounced callus formations accompanied by definite cankers and heavy flow of balsam from the region of inoculation.

TABLE 2.—*Results of cork-borer inoculations after 16 months*

Tree no.	Diameter breast high	Vigor	Borings	Bands	Condition [1]
	Inches		*Number*	*Number*	
1	4½	Medium	13	2	Dead.
2	3½	do	11	2	Normal.
3	5	do	13	3	Several dead branches.
4	2½	do	6	2	Dying.
5	2	Poor	5	2	Normal.
6	3½	Medium	11	1	Do.
7	3	Poor	14	2	Dead.
8	3½	Medium	11	2	Normal.
9	4	do	12	2	Do.
10	4½	do	16	2	Dead.

[1] Condition of all checks was normal.

Detailed examinations of all the inoculated trees showed that the cambium was killed as the fungus advanced and that when the stain had coalesced into a solid band extending completely around the tree trunks an effective girdle was formed. It was also found that when the inoculated trees did not show indicative dead branches in the crown the stain had failed to coalesce in one or more places on the trunks; hence the girdles were not complete, and the trees survived. It should be mentioned, however, that before any of the inoculated trees succumbed *Scolytus* beetles had attacked the trunks above the girdles and probably hastened the death of the trees. Figure 7 shows the appearance of an inoculated tree trunk at the conclusion of the test. The checks remained in normal condition throughout the entire period.

From these tests it may be concluded that *Trichosporium symbioticum* is definitely pathogenic. Mechanical wounds, such as those pro-

vided by the beetle galleries, may aid the fungus in becoming established but are not essential for the extension of the hyphae. The fungus, spreading ahead of the galleries in beetle-infested trees, kills the cambium as it advances. When the stain coalesces to form large areas, spreading from one gallery to another, it produces a more effective girdle than would the galleries alone.

Others have also shown that wood-staining organisms may be parasitic on the host. Münch (*11*) concluded that under certain conditions the bluing fungi, with which he worked, may cause the death of pine trees. Nelson and Beal (*12*), working with southern pine in this country, showed that the blue stains associated with *Dendroctonus frontalis* Hopk. may play an important part in killing infested trees. The organisms studied by the above workers did not belong in the genus *Trichosporium*, but other investigators have indicated certain of these species to be parasitic as well. Butler (*5*) found *T. resiculosum* Butl. associated with the death of casuarina trees in India. He found that the hyphae lie within the vessels and bore their way through intervening cell walls. In other instances, species of *Trichosporium* have been indicated to be parasitic, such as *T. parasiticum* Dearn. and Bisby (*4*) on *Amelanchier alnifolia* Nutt. leaves.

Since stain development precedes the appearance of the larvae, it may be that the fungus aids the brood by adjusting localized conditions. This seems to be particularly pertinent in isolated galleries, such as overcome attacks, where the host tree remains alive but the larvae thrive.

The killing of the cambial region probably restricts the flow of balsam, or the hyphae of *Trichosporium symbioticum* may render certain food products more digestible, as shown by Heitz (*8*) and others for other fungi. The effect of the stain on moisture conditions may also be of particular importance, as suggested by Struble,[9] since the larvae have never been found in unstained material. It appears desirable, therefore, to determine what effect the fungus may have on moisture conditions within infected areas.

MOISTURE RELATIONSHIP TESTS

The cork-borer method was employed again to construct a partial band of *Trichosporium symbioticum* inoculations extending around only one-quarter of the circumference of several trees. Two rings were spaced 2 inches apart and the borings of the lower ring alternated with those above, as described before. Ten white firs were inoculated in this manner, and the disks were sealed in place with adhesive tape.

These inoculations were made in late June and were not disturbed for 2 weeks since a similar length of time elapses between the initiation of a *Scolytus ventralis* attack and the appearance of the first larvae. At that time the adhesive tape was removed and a 1-inch arch punch [10] was driven through the bark between the inoculation rings and into the sapwood where the stain would be coalesced. In this manner a core of stained wood and overlying bark was readily removed from five inoculated trees and to prevent desiccation was

[9] See footnote 3.

[10] An arch punch is a steel tool used in the leather trade. It has a sharp, hollow, circular blade over which the handle arches; hence the name.

wrapped in tin foil before being deposited in a container which was then tightly closed. Similar cores of fresh unstained wood were extracted about an inch from the end of the inoculated areas. Since the discoloration does not penetrate deeper than the current growth ring, the specimens were trimmed down to the thickness of one ring and the bark was removed before weighing. The cores were dried at 100° C. until a constant weight was obtained for each sample, and the percentage of moisture was determined on a dry-weight basis. Table 3 summarizes the comparative results of the final weighings.

TABLE 3.—*Comparison of moisture in stained and unstained white fir wood 2 weeks after inoculation*

Tree no.	Diameter breast high	Unstained wood			Stained wood			Difference in moisture
		Wet weight	Dry weight	Moisture [1]	Wet weight	Dry weight	Moisture [1]	
	Inches	*Grams*	*Grams*	*Percent*	*Grams*	*Grams*	*Percent*	*Percent*
11	9	1.321	0.434	204	1.128	0.569	98	−106
12	7	1.388	.484	187	.618	.320	93	−94
13	6	1.474	.482	206	1.550	.672	131	−75
14	8	1.753	.599	193	1.788	.760	135	−58
15	7	2.134	.684	212	2.050	.920	123	−89
Average	7.4	1.614	.536	200	1.427	.648	116	−84

[1] Percentage of moisture based on dry weight.

After 2 months it was found that the moisture in stained samples from five other white firs still averaged 88 percent less than that of unstained wood taken from the same trees.

It is known that moisture fluctuates considerably in individual trees, depending upon the time of the day and the season, and that there may also be variations even in the same tree trunk, particularly with reference to the circumference. These percentages are, therefore, presented as approximate rather than absolute. The fact remains, however, that *Trichosporium symbioticum* does reduce the moisture conditions locally and that the beetle larvae develop where moisture is less than in adjacent unstained areas, since their galleries occur only in association with the discoloration. It is not impossible that the fungus may consequently render conditions more favorable for the successful development of the larvae and particularly aid in the preservation of isolated colonies.

CONCLUSIONS

On the basis of the data collected, the writer suggests that the relationship of *Trichosporium symbioticum*, n. sp., to *Scolytus ventralis* Lec. may be one of mutual advantage.

The beetle benefits, since the fungus kills the cambium as it advances and thereby assists in overcoming the host tree. The fungus reduces the moisture content of the cambial region ahead of the larvae and in this way may render conditions more favorable for their development.

The fungus benefits, since it is carried by the beetles to new and suitable substrata, presumably otherwise unattainable, where it is able to maintain and reproduce itself. The association appears to be symbiotic.

SUMMARY

A fungus has been frequently isolated from a number of brown-stained areas associated with *Scolytus ventralis* Lec. galleries. The isolated organism has been determined as *Trichosporium symbioticum*, n. sp.

The stain is regularly associated with *S. ventralis* galleries in white firs and has always been observed to precede the appearance of the larvae.

S. ventralis adults carry *T. symbioticum*, mostly epizoically, and in this way presumably spread the fungus from infected to noninfected trees.

A cork-borer method of inoculation has shown that *T. symbioticum* is definitely pathogenic and capable of killing the cambium as it advances. In this way it may aid the beetles in overcoming the host trees. The hyphae, spreading ahead of the larvae, reduce the moisture content of the areas in which the larvae extend their mines.

The regular association of *T. symbioticum* with *S. ventralis* appears to be one of mutual benefit and suggests a symbiotic relationship.

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A COMPARATIVE STUDY OF CERTAIN MORPHOLOGICAL CHARACTERS OF SUGARCANE × SORGO HYBRIDS [1]

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INTRODUCTION

Breeding work was initiated by the writer (*3, Rept. 45*)[2] in the fall of 1930 for the special purpose of obtaining crosses between sugarcane, *Saccharum officinarum* L., and sorgo (sweet sorghum), *Holcus sorghum* L. var. *saccharatus* (L.) Bailey. Earlier in the same year Thomas and Venkatraman (*14*) announced that they had succeeded in securing crosses between sugarcane and *Sorghum durra* Stapf. The first attempt to obtain crosses in Florida proved unsuccessful and led to a detailed study of the mechanics of cross-pollination under local conditions, the main results of which will be reported briefly. Since sugarcane blooms in this hemisphere only when daily illumination is short, starting usually in late November or early December and lasting until late February, this intergeneric cross can only be effected each year during this particular period in the annual cycle.

During the flowering season of 1931–32, the cross was again attempted. Certain information gained in the previous trials was used, and approximately 145 hybrids were secured, only 69 of which were actually set in the field for growth to maturity, as previously reported by the writer (*3, Rept. 46*). Six of those set in the field failed to reach maturity, so that only 63 were available for study, 24 being of the cross P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo, and 39 of the cross P. O. J. 2725 sugarcane × Early (Kansas) Orange sorgo.

During the flowering season of 1932–33 the crossing work was repeated, and approximately 200 hybrids were secured. Of these, 84 of the cross P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo and only 6 of P. O. J. 2725 sugarcane × Sugar Drip Sorgo reached the potted stage and were planted in the field. Further deaths in the field reduced the total number of hybrids reaching maturity in this series to 65.

It is therefore seen that the total number of hybrids grown to maturity was 128 from a total population germinated in the seed bed of 345, or only 37 percent. The majority of the young plants, including a number of albino types, died shortly after germination, apparently due to genetic weakness or incompatibility.

During the flowering season of 1931–32, the reverse cross—Texas Seeded Ribbon sorgo (female) × C. P. 27–35 [3] (male) sugarcane was attempted. In this trial, 97 sorgo flowers were carefully emasculated just before the spikelets reached maturity, and dusting with sugar-

[1] Received for publication July 19, 1934; issued May 1935.

[2] Reference is made by number (italic) to Literature Cited, p. 551.

[3] A male parent having an abundance of healthy pollen. This sugarcane is a cross between D. 74 (female) × U. S. 1694 (male), produced by the writer at the U. S. Sugar Plant Field Station at Canal Point, Fla., in 1927.

cane pollen was carried out in an isolated area free from sorgo pollen. This single reciprocal crossing trial, however, resulted in failure.

MATERIALS AND METHODS

In the main, the hybrid material used for the studies here reported consisted of crosses between P. O. J. 2725 sugarcane (female) × Texas Seeded Ribbon sorgo (male). The plants were grown on Okeechobee muck soil adjacent to plots of the parental types at Lake Harbor, Fla. The age of the hybrids and of P. O. J. 2725 sugarcane grown for comparison was approximately 1 year from the germination of seeds and cuttings, respectively. The sorgo plants grown for comparison, however, were almost 4 months old from seed planted in the fall and grown during the cool, dry winter months when the daily illumination is short. Comparisons have not been made of hybrids with sorgo plants grown during the warm, moist spring and summer months when the daily illumination is long.

The sugarcane variety P. O. J. 2725, used as a female parent in the hybridization experiments was previously found to be almost completely male sterile in repeated trials. Occasionally 1 or 2 seedlings have been produced per tassel under conditions where cross-pollination was impossible.

Physiological studies on the germination of sugarcane and sorgo pollen were conducted similar to those on sugarcane pollen by Dutt and Ganapathi Ayyar (*6*) and Weller (*16*). It was found that the best artificial medium on which to germinate sorgo pollen at 23° C—the temperature at which all comparative trials were made—consisted of 34 g of sucrose, 66 g of distilled water, and 0.3 g of agar. The medium when made up had a reaction of pH 5.6. Weller (*16*) found that the best artificial medium for the germination of sugarcane pollen in Hawaii consisted of sucrose 25.0 g, water 100.0 cc, and agar 0.35 g. This medium, which contains 19.5 percent sucrose, was found to germinate the pollen of several varieties of sugarcane grown locally. Since the medium used by Dutt and Ganapathi Ayyar (*6*) for germinating sugarcane pollen contained 26 percent sucrose and 0.7 percent agar, it would appear that the optimum medium for the germination of sugarcane pollen varies according to the climatic conditions under which the plants are grown. The data also suggest that even different sugarcane varieties may have different medium preferences under uniform external environmental conditions. A comparison of the results with the germination of sugarcane pollen from India and Hawaii would also tend to explain the success with the intergeneric cross between sugarcane and sorgo in the former country, since it is evident that sugarcane stigmas in India have an osmotic pressure very much nearer the optimum for sorgo pollen germination than in either Hawaii or this part of Florida.

Basing calculations on the researches of Frazer and Myrick (*7*) on the osmotic pressure of sucrose solutions, it was found that the medium suitable for the germination of local sugarcane pollen at 23° C. has an approximate osmotic pressure of 18.5 atmospheres and that for sorgo pollen, 41.5 atmospheres. The experimental evidence indicates clearly, therefore, that for success in effecting cross-pollination of sugarcane and sorgo, the medium on the sugarcane stigmas should have its osmotic pressure more than doubled in order to provide an

ideal physical environment for the sorgo pollen to germinate under local conditions.

In all the germination studies with local sorgo pollen it was found that while good germination was secured with cells shed between 6 and 8 a. m., the percentage of germination fell off rapidly after 8 a. m. Although no actual germination trials were reported by McIntosh (*12*), this author showed that the optimum period for pollen shedding of sugarcane in Barbados is between 7 and 8:30 a. m. This period agrees fairly well with that at which sorgo pollen germinates best locally.

For effecting cross-pollination between sugarcane and sorgo, the sugarcane tassels were bagged from late evening until about 10 a. m. each day throughout the flowering period, so as to exclude rain and

FIGURE 1.—General view of a portion of seedling field showing hybrids of P. O. J. 2725 sugarcane × *Holcus sorghum* var. *saccharatus*. Age of plants about 1 year from the germination of seed. In the back ground at the left is a sugarcane plot which has arrowed.

dew and prevent reduction in osmotic pressure of the stigma fluid. The sorgo pollen was dusted on the tassels under the bags between 6 and 8 a. m. After the pollination period of about 10 days was over, the sugarcane tassels were allowed to ripen normally in the open, this operation usually requiring approximately 4 weeks.

For germinating the mature seeds, only steam-sterilized muck soil and flats were employed, and the most favorable conditions of moisture, temperature, and greenhouse protection were provided.

The method of selecting, preparing, and staining epidermal material for anatomical characters was essentially the same as that used by Artschwager (*1*). The staining of the epidermis of the stem of sorgo with chloroiodide of zinc had to be performed under cover glasses because of the marked tendency of films to curl rapidly.

In order to obtain an estimate of the variance occurring among hybrid populations and parent plants in those factors studied, a determination was made of the standard error of the means with a

view to providing evidence of significance where this occurred. The usual formula, $\frac{\sigma}{\sqrt{n}}$, was used in all the calculations reported.

COMPARISON OF GENERAL CHARACTERS OF P. O. J. 2725 SUGARCANE × TEXAS SEEDED RIBBON SORGO HYBRIDS WITH THEIR PARENTS

Figure 1 gives a general view of a portion of a seedling plot of sugarcane × sorgo hybrids (P. O. J. 2725 sugarcane × *Holcus sorghum*

FIGURE 2.—One of the best selections of the cross P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo in bloom. This is selection F. 32-47.

var. *saccharatus*) about a year after the germination of the seed. In general appearance these resemble the hybrids between P. O. J. 2725 sugarcane × *Sorghum durra* produced by Venkatraman and Thomas (*15*). As may be observed, a majority of them are dwarfed types which do not appear promising for commercial utilization.

Only about 3 percent showed enough vigor and field characters of sufficient promise to be considered for further trials. One of the types, selection F. 32–47, selected for propagation and testing, is shown in figure 2. About 1 percent of the population consisted of types which could not be distinguished from true sugarcane seedlings. These latter might have been produced either parthenogenetically or through normal selfing.

WIDTH OF LEAVES

Venkatraman and Thomas (*15*) have already noted certain characters, such as shortness, softness, and light green color of leaves of hybrids between P. O. J. 2725 sugarcane and *Sorghum durra*. Considerable variation was noted in regard to these same characters among the progeny of P. O. J. 2725 sugarcane × *Holcus sorghum* var. *saccharatus*, representing almost a complete series from one parent to the other. Leaf width was studied in a population of 59 crosses between P. O. J. 2725 sugarcane and Texas Seeded Ribbon sorgo. The number of progenies having leaf widths falling in eight groups is recorded in table 1. The modal class of progenies occurred in the 4.5-cm group. The average of all progenies was 4.95 ± 0.17 cm, while the average leaf width of P. O. J. 2725 sugarcane and Texas Seeded Ribbon sorgo planted on the same soil type and at the same time was 8.2 ± 0.31 cm and 2.8 ± 0.07 cm respectively. Thus the average width of the leaves of the hybrid progeny is not significantly greater or less than the average of the two parents.

TABLE 1.—*Grouping of hybrids between P. O. J. 2725 sugarcane and Texas Seeded Ribbon sorgo according to leaf width*[1] *(59 hybrids), height*[2] *(58 hybrids), and stem width (49 hybrids)*

LEAF WIDTH

Item	Number falling in class (cm) indicated							
	1.75	2.5	3.5	4.5	5.5	6.5	7.5	8.5
Progeny	1	3	8	22	14	7	3	1

HEIGHT

	10	30	50	70	90	110	130	150	170	190	210	230	250	270
Progeny	2	18	6	13	7	3	4	1	2	0	0	1	0	1

STEM WIDTH

	1.25	1.75	2.25	2.75	3.25
Progeny	6	18	10	12	3

[1] Measurements made in the middle of blade at point giving the maximum width; approximately 10 leaves of each hybrid were measured.
[2] Average of all primary shoots measured from base to sheath-blade joint of the first expanded apical leaf.

HEIGHT OF PLANTS

It has already been noted that the majority of the sugarcane × sorgo hybrids that grow are rather stunted and not commercially promising in appearance. In order to gain a better idea of the varia-

bility within a population of a given cross, the height of 58 progenies of P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo was studied when the plants had matured, which was about 1 year after the germination of the seed. The height of all the primary shoots was found by measuring from the base to the sheath-blade joint of the first expanded apical leaf. The number of plants falling in 14 groups and the modal class are recorded in table 1.

The results show that the modal class of progenies, or 31 percent, fell in the group of 30 cm height. The next largest percentage (22 percent) fell in the group of 70 cm. Variations from 15–280 cm were recorded, the average of all 58 progenies being 75.7 ± 6.7 cm.

Texas Seeded Ribbon sorgo grown at the same time and on the same soil type (growth period from October to February) averaged 150.0 ± 5.3 cm in height when in bloom. Normal P. O. J. 2725 sugarcane, as first crop or plant cane of the same age as the hybrids and growing on the same soil type in an adjoining plot, averaged 316.0 ± 13.8 cm in height. Thus the average height of the two parents was nearly three times that of the average of the 58 progenies resulting from the crossing of these parents. Had the sorgo for this comparison been grown in the spring and summer, instead of fall and winter, when opposite conditions of moisture, temperature, and duration of daily illumination occur, very different results, and results of even greater significance, might probably have been obtained.

DIAMETER AND OTHER CHARACTERS OF STEMS

There is almost a complete series of variations in stem characters among the hybrids, ranging from those resembling sugarcane to those resembling sorgo. Stalk diameter, shape of bud, width of root band, and depth and extent of bud grooves on the stem internodes vary to a considerable extent. Typical variations in all of these characters are shown in figure 3. The bud groove on the internode, a very prominent character of the sorgo parent only, appeared to be one of the most dominant characters. Among 47 progenies of P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo, 41 exhibited marked grooves, while only 4 showed slight grooves and 2 showed none.

A study was made of 49 progenies of P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo with regard to diameter of stalk midway between the apex and base. The number of progenies falling in each of five groups is recorded in table 1. The modal class occurred in the 1.75-cm group. The average of all 49 progenies was 2.23 ± 0.08 cm, while that of P. O. J. 2725 sugarcane was 3.23 ± 0.05 cm and that of Texas Seeded Ribbon sorgo was 1.26 ± 0.07 cm. The average for the two parents was 2.24 ± 0.12 cm. Thus, the stalk diameter of the progeny of this cross was, on an average, intermediate between that of the two parents, with some extremes occurring in the groups nearest sugarcane and some in the groups nearest sorgo.

PECULIARITIES OF INFLORESCENCES

As in the case of sugarcane, hybrids which "boented" [4] or bloomed did so only during that period in the annual cycle in which daily illumination was short. Relatively few hybrids have so far produced

[4] This is a term frequently used in sugarcane literature when referring to the tapered or spiked appearance of the apical growing point of the stalk prior to the emergence of the inflorescence.

FIGURE 3.—Middle stalk portions of four sugarcane × sorgo hybrids: *A*, F. 31-61 (P. O. J. 2725 × Early Orange); *B*, F. 31-6; *C*, F. 31-10; *D*, F. 31-13 (P. O. J. 2725 × Texas Seeded Ribbon). The first two have very shallow furrows which extend about halfway between nodes as in the case of the sugarcane parent P. O. J. 2725. The last two have narrow but very deep furrows, which frequently extend from node to node as in the case of the sorgo parent, Texas Seeded Ribbon sorgo.

inflorescences, although many have boented during the past two tasseling seasons. Typical blooms of four different hybrids are shown in figure 4. Among these, the strain F. 31–13, resulting from the cross P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo (figure 4, *C*), grown in 1932, showed many of the interesting characters reported by Venkatraman and Thomas (*15*) for certain seedlings of the cross P. O. J. 2725 sugarcane × *Sorghum durra*. These authors mention that 22 percent of their hybrids that arrowed showed an awned fourth glume as well as such abnormalities as aborted or multiple ovaries and pistils with a single stigma or with four stigmas. So far as the writer is aware, this is the first record of a four-stigma

FIGURE 4.—Blooms of four sugarcane × sorgo hybrids: *A*, Tassel of F. 31–30 (P. O. J. 2725 sugarcane × Early Orange sorgo); *B*, tassel of F. 31–10 (P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo); *C*, tassel of F. 31–13; *D*, tassel of F. 31–29, both *C* and *D* being P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo.

floret or of a multiple ovary among those members of the Gramineae which possess uniflorous spikelets. Hitchcock, in Gray's New Manual of Botany (*8*), records only the rare occurrence of 1 to 3 styles to the pistil among the Gramineae and apparently has never observed any variation whatever from the single pistil with its one-celled, one-ovuled ovary in each floret.

The occurrence of multiple ovaries is to be distinguished from true polyembryony, an instance of which has recently been noted by Dutt (*5*) in a cross between two sugarcanes.

Stratton (*13*) has shown that while each spikelet in *Zea mays* normally bears two flowers, one functional and the other aborted, in *Z. mays* var. *polysperma*, both flowers may function to produce either a pair of separate connate seeds (kernels back to back) or semiconnate seeds. A condition of abnormal spikelets similar to that in *Z. mays*

var. *polysperma* has also been noted by Karper (*11*) in the case of *Andropogon sorghum*, good evidence being furnished that the extra kernels arose from additional functional flowers within the spikelet. It should be noted especially, however, that Karper recorded spikelets with twin seeds, coalesced twin seeds, and triplet seeds among several varieties of grain sorghum, but did not find any multiple-seeded spikelets among sorgo varieties. The presence of multiple seeded spikelets in both *Z. mays* var. *polysperma* and *A. sorghum* should not be confused with the situation occurring in the hybrid F. 31–13, however, for in the latter case, each spikelet is uniflorous, exactly as in sugarcane, and does not possess additional aborted flowers, so that a multiple ovary, or a biovaried condition, as well as the occurrence of three or more styles or stigmas to the floret must be regarded as being especially significant.

Structure of Spikelets of Parents

In P. O. J. 2725 sugarcane, two uniflorous spikelets are alternately placed at the nodes of the rachis, one being sessile and the other stalked. Both spikelets are oblong and lanceolate and possess tufts of long, silky hair at their base. A cross section of a spikelet of P. O. J. 2725 sugarcane, illustrated in plate 1, *B*, also shows that this variety is normal and identical in structure with many varieties of *Saccharum officinarum*. There are present an outer and an inner glume, a sterile lemma (third glume), fertile palea, 2 thick lodicules, 3 stamens, and a single ovary. The fertile lemma (fourth glume), mentioned by Artschwager et al. (*1*) as being present in the hybrids of *S. spontaneum*, is absent, in spite of the fact that this variety has approximately one-eighth *S. spontaneum* blood (*10*). In the Andropogoneae, the tribe in which sugarcane is placed, Jeswiet (*9*) states that the fourth glume (g_4) is very rarely missing and is also generally present in the genus *Saccharum*, although in a great many varieties of *S. officinarum* it is absent.

The structure of the spikelet in Texas Seeded Ribbon sorgo has been described by Cowgill (*4*). The fertile spikelet in this variety has outer and inner glumes, sterile lemma, fertile lemma with awn medium in length and somewhat loosely twisted, 2 lodicules, a fertile palea, 3 stamens, and a single ovary. As compared with sugarcane spikelets, those of all sorgo varieties have a much greater diameter.

Structure of Spikelets of Hybrid F. 31–13

Like sugarcane, the hybrid F. 31–13 (P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo) has two uniflorous spikelets alternately placed at the nodes of the rachis, one sessile and the other stalked. The spikelets are oblong and lanceolate and possess tufts of long, silky hairs at the base. As recorded by Venkatraman and Thomas (*15*) for 22 percent of their sugarcane × sorghum hybrids that arrowed, F. 31–13 showed an awned fourth glume or fertile lemma, as illustrated in plate 2, *A*. The awn is characteristically curved and is distinctly longer than the fertile lemma. While many flowers possess 2 purplish stigmas, very frequently 3 and 4 (pl. 3, *A*, *B*), and occasionally even 5, stigmas occur. Spikelets (uniflorous) with 4 or 5 stigmas possess two distinct ovaries, as illustrated in plate 3, *A*. Serial microtomic

sections show that when a biovaried condition occurs, one ovary may have its ovule wanting (pl. 2, *B*). In addition to the foregoing parts, this hybrid has outer and inner glumes, a sterile lemma, a fertile palea, 2 lodicules, and 3 anthers (stamens), as shown in plate 1, *A*. While in sugarcane the sterile lemma has been noted by Jeswiet (*9*) to be mostly without nerves or vascular bundles, and Artschwager et al. (*2*) state that the fertile lemma, if present, has no vascular elements, both the sterile and fertile lemmas of the hybrid F. 31–13 are nerved (pls. 1, *A*, and 2, *A*). The palea, however, is without vascular elements, which is in accord with the condition existing in the genus *Saccharum*. No flowers were observed to possess more than 3 anthers, even though they had more than 2 styles and stigmas as well as 2 ovaries.

Venkatraman and Thomas (*15*) mention that the glumes of P. O. J. 2725 sugarcane and its sugarcane hybrids as well as *S. spontaneum* are awnless, whereas *Sorghum durra* possesses a distinctly awned fourth glume. The same condition of an awned fertile lemma or fourth glume exists in *Holcus sorghum saccharatus*, variety Texas Seeded Ribbon, and it is therefore not surprising that the hybrid F. 31–13 exhibits this character. Jeswiet (*9*) records the frequent occurrence of a shorter or longer awn or needle among the Andropogoneae. He states that sometimes this needle is all there is and it may vary in length from a fraction of a millimeter to more than a decimeter.

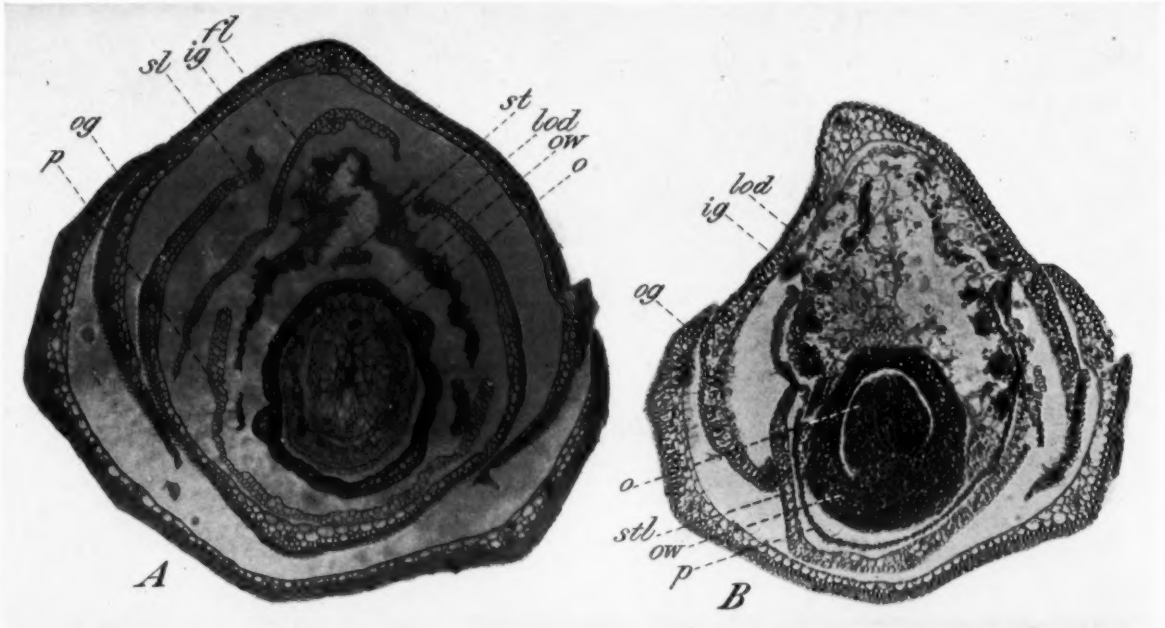
Plate 1, *A*, *B*, shows the diameter of the spikelet of the hybrid F. 31–13 to be significantly greater than that of the sugarcane parent P. O. J. 2725, undoubtedly due to the influence of the large diameter of the spikelets in the sorgo parent, Texas Seeded Ribbon.

The vascular system of the rachis in sugarcane below the cushion joint has been shown by Artschwager et al. (*2*), in the case of 1 variety, to consist of 2 large bundles toward the center and 3 smaller ones toward the outside. In the hybrid F. 31–13, when 3 styles, 3 stigmas, and a single ovary are present, there are 5 smaller bundles in addition to the 2 larger bundles.

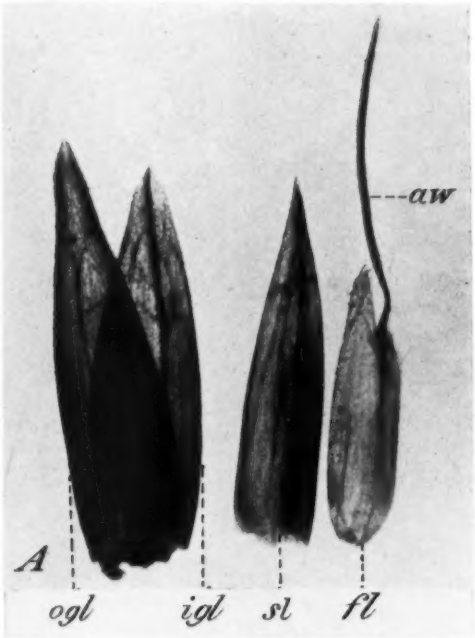
It has also been noted that the vascular system of the ovary wall of the hybrid F. 31–13 indicates clearly the number of styles and stigmas borne by the spikelet. In sugarcane, Artschwager et al. (*2*) note that the ovary wall has two fine lateral vascular strands running longitudinally through it. These, of course, are the strands which connect with the 2 styles and stigmas in the normal flower. In the hybrid F. 31–13, however, while the normal 2-stigma flower possesses 2 distinct vascular strands (pl. 1, *A*) in the ovary wall, the 3-stigma florets have 3 vascular strands in the ovary wall, and flowers having 5 stigmas have 2 ovaries, one with 3 and the other with 2 vascular elements (pl. 2, *B*).

CELL STRUCTURE OF STEM EPIDERMIS OF SEVERAL SUGARCANE × SORGO HYBRIDS AND THEIR PARENTS

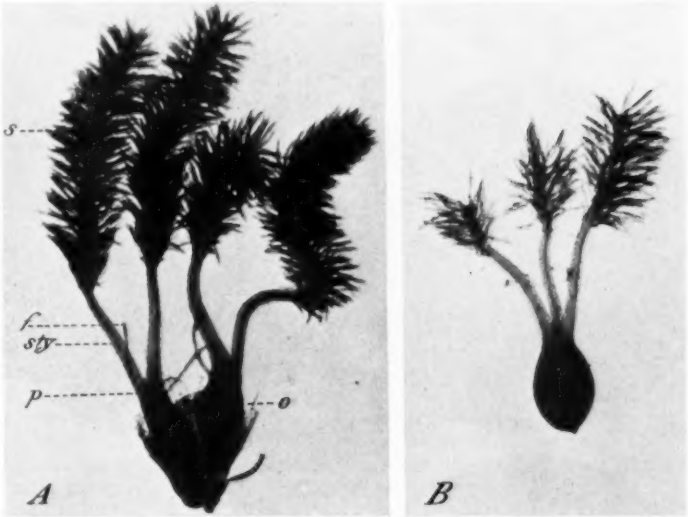
Owing to the great constancy of stem epidermal anatomical characters among different sugarcane varieties and their value for identification purposes (*1*), it was thought that a study of the influence of these parental characters on the hybrid progeny would prove of interest. Consequently, a detailed study was made of the stem epi-



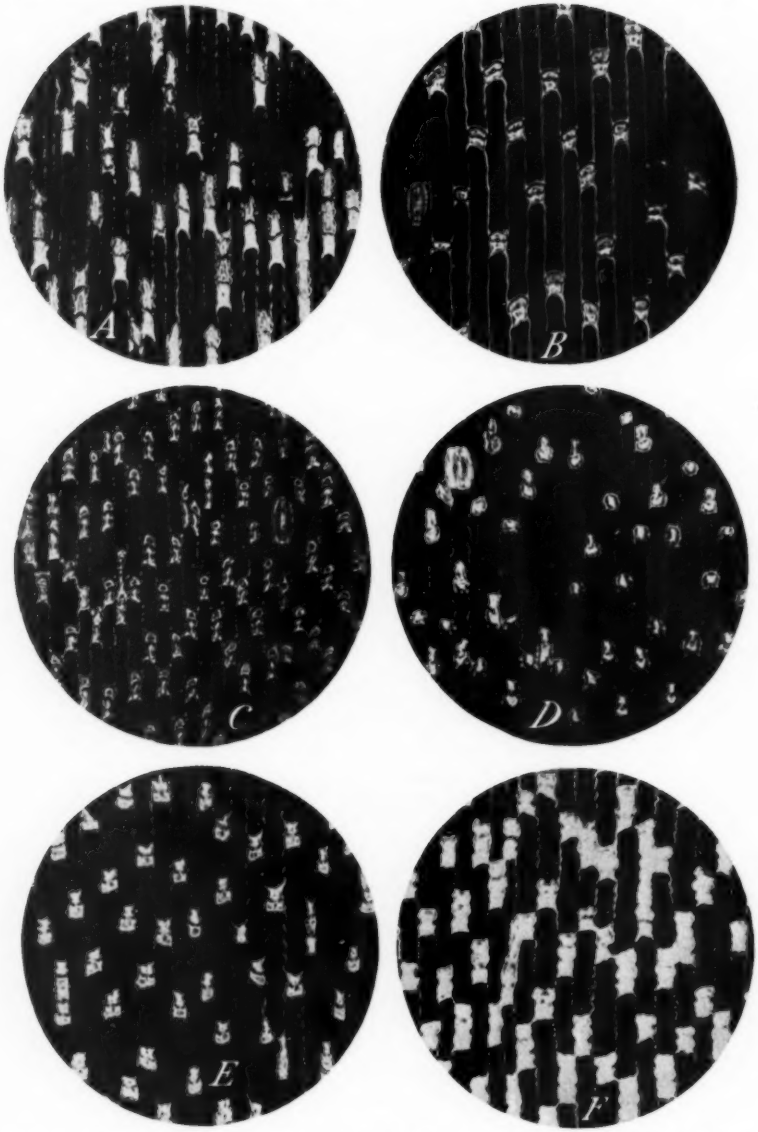
A, Cross section of normal spikelet of the hybrid F. 31-13, showing: *fl*, Fertile lemma; *ig*, inner glume; *sl*, sterile lemma; *og*, outer glume; *p*, palea; *lod*, lodicule; *ow*, ovary wall with two vascular strands; *o*, ovule, and *st*, stamen. × 105. *B*, Cross section of spikelet of P. O. J. 2725 sugarcane, showing: *lod*, Lodicule; *ig*, inner glume; *og*, outer glume; *o*, ovule; *ow*, ovary wall; *stl*, sterile lemma, and *p*, palea. × 105. Note the greater diameter of the sugarcane × sorgo hybrid spikelet as compared with that of sugarcane.



A, Portions of spikelet of F. 31–13, hybrid of P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo, showing: *ogl*, Outer glume; *igl*, inner glume; *sl*, sterile lemma; *fl*, fertile lemma; *aw*, awn of fertile lemma. × 14.1. *B*, Cross section through spikelet of the hybrid F. 31–13, showing two ovaries, one normal and the other aborted. This spikelet had five styles and stigmas. × 124.



A, Abnormal floret of the hybrid F. 31–13 showing two ovaries, four styles and stigmas: *s*, Stigma; *f*, anther filament; *sty*, style; *p*, palea; and *o*, ovary. × 19. *B*, Abnormal pistil of the hybrid F. 31–13 showing an ovary with three styles and stigmas. × 19.



Anatomical structure of epidermis of stems of sugarcane, sorgo, and several hybrids between the two parental types: *A*, P. O. J. 2725 sugarcane; *B*, Texas Seeded Ribbon sorgo; *C*, hybrid F. 31-29; *D*, hybrid F. 31-33 (note frequent occurrence of solitary cork cells); *E*, hybrid F. 31-13; *F*, hybrid F. 31-6. All × 214.

dermal anatomy of P. O. J. 2725 sugarcane, the two sorgo varieties, Texas Seeded Ribbon and Early (Kansas) Orange, and of several hybrids between each of the sorgo varieties and P. O. J. 2725 sugarcane, selected entirely at random. The results of this study are summarized in table 2.

TABLE 2.—*Epidermal characters of stem of sorgo, sugarcane, and several hybrids between these 2 grasses*

Variety [1]	Average width of cells	Short-cell groups per square millimeter	Stomata per microscopic field [2]	Pointed elongated cork cells	Solidary cork cells	Solitary silica cells
	μ	*Number*	*Number*			
Texas Seeded Ribbon sorgo.	12.1	[3] 545±25	27.0±0.10	Absent	Abundant	Rare.
Early Orange sorgo	10.7	1,033±27	95.0±9.1	do	Absent	Absent.
P. O. J. 2725 sugarcane	8.4	625±24	2.8±0.62	Very abundant	Very abundant	Rare.
F. 31–6	11.7	1,320±11	2.8±0.9	Present	Rare	Do.
F. 31–10	10.3	800±38	1 —	Scarce	do	Do.
F. 31–13	10.5	920±00	5.5±1.4	Absent	do	Do.
F. 31–29	10.4	1,512±76	36.0±0.94	do	do	Absent.
F. 31–33	10.4	950±31	13.4±2.5	Scarce	Very abundant	Rare.
F. 31–40	11.2	1,166±62	5.2±2.0	Absent	Rare	Do.
F. 31–61	10.6	850±00	25.5±0.35	Present	Abundant	Absent.

[1] F. 31–6, –10, and –13 are hybrids between Texas Seeded Ribbon sorgo (male) and P. O. J. 2725 sugarcane (female). Other F. 31 numbers are hybrids between Early (Kansas) Orange (male) and P. O. J. 2725 (female).

[2] Ocular × 10 and 16-mm objective, or 1.9 mm².

[3] Standard error of the mean of not less than 5 determinations.

The average width of the cells of P. O. J. 2725 sugarcane (pl. 4, *A*) is unusually small (8.4 *μ*), in this respect resembling the sugarcane varieties D. 74 and Chunnee. The number of stomata (2.8±0.62) per microscopic field is also small in this variety as compared with the number in the two sorgo varieties crossed with it, although such an occurrence is not at all unusual among sugarcane varieties. The great abundance of pointed, elongated cork cells in P. O. J. 2725 sugarcane and the complete absence of these in both of the sorgos, however, give contrasting characters of value for inheritance studies among the hybrid progeny.

The average widths of cells in the hybrid progeny F. 31–6 (pl. 4, *F*), F. 31–10, and F. 31–13 (pl. 4, *E*), crosses between P. O. J. 2725 sugarcane and Texas Seeded Ribbon sorgo, are all intermediate between those of the two parents. Similarly, the average widths of cells of the hybrid progeny F. 31–29 (pl. 4, *C*), F. 31–33 (pl. 4, *D*), and F. 31–61, crosses of P. O. J. 2725 sugarcane and Early Orange sorgo, are also intermediate between the two parents, F. 31–40 being the only one in this group with average cell width greater than that of Early Orange sorgo, the male parent.

In number of short-cell groups per square millimeter, all of the hybrids of both crosses were significantly greater than P. O. J. 2725 sugarcane, even though the Texas Seeded Ribbon sorgo parent (pl. 4, *B*) had less than P. O. J. 2725, the sugarcane parent. The fact that F. 31–6 had more than the sum of the two parents and F. 31–29 and F. 31–40 more than either parent, is also significant.

The number of stomata per microscopic field (1.9 mm²) is very high in both sorgo parents, especially in Early Orange. The average number of stomata per field among the four hybrids of P. O. J. 2725

sugarcane × Early Orange sorgo is 20.0±1.4, while the average of the three hybrids of P. O. J. 2725 × Texas Seeded Ribbon sorgo is only 3.1±1.1, showing the apparent dominance of the large number of stomata in Early Orange sorgo.

Pointed, elongated cork cells were very abundant in P. O. J. 2725 sugarcane and absent in both sorgo parents. These peculiar cells were never found very abundantly in the hybrids. More than half of the seven types examined had them, but in many cases they were rather scarce.

Although solitary cork cells are somewhat abundant in Texas Seeded Ribbon sorgo and very abundant in P. O. J. 2725 sugarcane, these cells occurred rarely in all three of the plants of this cross. On the other hand, although these solitary cork cells were absent in Early Orange sorgo, they were rather abundant in half of the hybrids with P. O. J. 2725 sugarcane, particularly in F. 31–33 (pl. 4, *D*).

The occurrence of solitary silica cells in the hybrids is in accordance with expectations. All the hybrids of P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo had them rarely, as did both parents, while in the case of hybrids of P. O. J. 2725 sugarcane × Early Orange sorgo, which lacks these cells, 50 percent had none and in 50 percent they occurred rarely.

SUMMARY

A brief review is given of the successful efforts to secure sugarcane × sorgo hybrids in Florida since 1930.

Some of the essentials for success in crossing sugarcane and sorgo in the Florida Everglades are pointed out; these are based on physiological studies of both sugarcane and sorgo pollen.

Of 345 hydrids produced thus far, only 128 have been raised to maturity. About 3 percent of these have shown enough vigor to warrant further field trials.

A comparative study has been made of the parents and hybrids as to leaf width, diameter of stem, height of plant, type of inflorescence and flower structure, when grown simultaneously under the same environment.

The hybrids of P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo were, on an average, intermediate between the parents in leaf width and stem diameter. The hybrid plants showed a wide variation in height, but the average height was significantly less than that of either parent.

The hybrid F. 31–13 showed several flower structures which were not found in either parent. The most conspicuous of these are an awned fertile lemma, 2 ovaries, and 3, 4, and even 5 styles and stigmas to the floret.

The average width of epidermal cells of the stems of hybrids resulting from crosses between P. O. J. 2725 sugarcane and Texas Seeded Ribbon sorgo and between P. O. J. 2725 sugarcane and Early Orange sorgo, is intermediate between those of the parents, in the majority of cases investigated.

All of the hybrids of both crosses investigated had a greater number of short-cell groups per square millimeter of the stem epidermis than the sugarcane parent P. O. J. 2725, even when the sorgo parent had fewer than the sugarcane with which it was crossed. One hybrid

had significantly more short-celled groups than the sum of the 2 parents, and 2 hybrids had more than either parent.

The average number of stem stomata per microscopic field of hybrids of P. O. J. 2725 sugarcane and Early Orange sorgo was significantly greater than that of hybrids of P. O. J. 2725 sugarcane and Texas Seeded Ribbon sorgo. This is attributed to the very large number of stem stomata per unit area in Early Orange sorgo.

Pointed, elongated cork cells were not abundant in the stem epidermis of any of the hybrids examined, these cells being absent in both sorgo parents but occurring very abundantly in P. O. J. 2725 sugarcane.

Solitary cork cells occurred rarely in the stem epidermis of all three of the hybrids of P. O. J. 2725 sugarcane × Texas Seeded Ribbon sorgo, although they were abundant in both parents. On the other hand, half of the hybrids of P. O. J. 2725 sugarcane × Early Orange sorgo had an abundance of solitary stem epidermal cork cells, although these cells were absent in Early Orange sorgo.

P. O. J. 2725 sugarcane, Texas Seeded Ribbon sorgo, and all the hybrids between these two parents rarely exhibited solitary silica cells in the stem epidermis. Fifty percent of the hybrids between P. O. J. 2725 sugarcane and Early Orange sorgo rarely showed solitary silica cells in the epidermis; the other 50 percent of the hybrids and the Early Orange sorgo parent lacked these cells entirely.

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THE EFFECT OF MAGNESIUM DEFICIENCY ON CROP PLANTS[1]

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INTRODUCTION

In 1891 a field experiment was started at the Massachusetts Agricultural Experiment Station for the purpose of testing fertilizers for corn (*Zea mays* L.). From 1891 to 1929 the cropping system varied somewhat, but for most of this period it consisted of a short rotation of corn and grass; 2 years of corn followed by 2 years of mixed grasses. During this period plant nutrients were supplied solely by commercial fertilizers, and none of these carried appreciable amounts of magnesium. One-half the experimental field received lime in 1907 and again in 1921. No record was made of the magnesium content of the lime, although it was no doubt appreciable. The soil is a well-drained sandy loam with a gravelly subsoil of the Merrimac series. Variations in topography and mechanical composition combine to produce heterogeneous soil conditions which cause results in dry seasons considerably different from those in wet seasons.

Chlorosis was first observed in the leaves of corn grown on this field about 1920. By means of experiments conducted during the period 1924–28 Jones [2] proved that this chlorosis was due to a deficiency of available magnesium in the soil. In 1929 a new experiment was started on the same field for the purpose of determining the relative response of the more common crop plants to the deficiency of magnesium, and to observe and record the plant symptoms produced by this deficiency.

PROCEDURE

From 1929 to 1934, inclusive, 17 varieties of crops were grown. In addition, tobacco had been grown in the earlier period, and red clover and alfalfa were grown in pots filled with soil taken from the magnesium-deficient section of the experimental field.

Prior to 1929 the fertilizer treatments of the four plots into which the field was divided varied considerably. Details of these treatments were reported in an earlier publication.[3] Beginning with 1929, the field was given annual applications of a 5-8-7 [4] fertilizer, but the rate at which this was used varied with the crop grown. Lime and magnesium treatments cut across the original fertilizer plots. The fertilizer, lime, and magnesium sulphate treatments for the period 1929–34 are given in table 1. The identity of the original plots was

[1] Received for publication Jan. 21, 1935; issued May 1935. Published as contribution no. 212 of the Massachusetts Agricultural Experiment Station.

[3] JONES, J. P. DEFICIENCY OF MAGNESIUM THE CAUSE OF CHLOROSIS IN CORN. Jour. Agr. Research 39:873–892, illus. 1929.

[2] JONES, J. P. See footnote 2.

[4] Figures refer to the percentage of N, available P_2O_5, and water-soluble K_2O.

preserved, and it was found that previous fertilizer treatments affected the yield of crops during the last period. From 5 to 10 varieties of crops were grown on each of the original plots, thus giving four replicates [5] of each variety. Individual plots varied from one three hundred and twentieth to one-eightieth acre in size. The original plots were given cross treatments of technically pure magnesium sulphate as shown in table 1. Field corn, variety Rustler's White Dent, which normally produces husking ears in this locality, was grown on each plot each year, and thus served as a standard for comparison with other crops. Counts of chlorotic corn plants were made each season.

TABLE 1.—*Fertilizer, magnesium sulphate, and lime added to the soil from 1929 to 1934*

Year	Crops	Fertilizer,[1] per acre	Other materials
		Pounds	
1929	Corn	800	Magnesium sulphate, 400 pounds per acre to section C [2] only.
	Timothy	500	
	Clover (alsike)	500	
	Potatoes	2,000	
	Onions	2,500	
1930	Corn	800	Do.
	Clover (alsike)	500	
	Timothy	500	
	Potaotes	2,000	
	Onions	2,500	
1931	Corn	800	No magnesium sulphate applied this year.
	Clover (alsike)	500	
	Timothy	500	
	Potatoes	2,000	
	Onions	2,500	
1932	Soybeans	800	Magnesium sulphate, 400 pounds per acre to sections B and C, and 1 ton low-magnesium (1.29 percent MgO) ground limestone per acre to sections A and B in fall.
	Clover (alsike)	500	
	Buckwheat	800	
	Soybeans	800	
	Corn	1,000	
	Oats	800	
1933 [3]	Oats	800	No magnesium sulphate applied this year.
	Barley	800	
	Sudan grass	800	
	Japanese millet	800	
	Rutabagas	1,500	
	Corn	1,000	
	Buckwheat	800	
1934 [3]	Pigweed	800	Magnesium sulphate, 100 pounds per acre applied to sections B and C.
	Barley	800	
	Rye	800	
	Field corn	1,000	
	Sweet corn	1,000	
	Japanese millet	800	
	Sudan grass	800	
	Rutabagas	1,600	
	Peppers	800	
	Mangels	1,600	
	Spinach	800	
	Turnips	800	

[1] 5–8–7 analysis.

[2] In the course of the experiment section A received lime; section B, lime and magnesium sulphate; section C, magnesium sulphate; section D, nothing except fertilizer which was applied to all sections.

[3] Ammophos was used instead of superphosphate to supply P_2O_5 for 1933 and 1934.

[5] Beginning with 1933, the east half of plot 1 was reserved for another experiment, thus reducing the number of replicates of some varieties to 3

EXPERIMENTAL RESULTS

YIELDS

The figures for yield are given in table 2. The annual precipitation records for Amherst, Mass., for the period May to August, inclusive, are as follows:

	Inches		Inches
1929	9.47	1933	14.25
1930	14.13	1934	12.84
1931	22.12	Mean (1889–1928)	15.74
1932	10.79		

Both season and variety were important factors in determining the results. The season of 1929 was abnormally dry and that of 1931 abnormally wet, each varying about 6.4 inches from the normal. These abnormalities depressed the actual yields. More significance should be attached to the corn crop than to any other because of its more frequent use in the experiment. The greatest relative effect of magnesium on the yield of grain corn was in 1931, a wet year, while one of the lowest relative yields of this crop was in the dry year 1929. The same order of agreement, however, does not hold for stover, but as Jones [6] has pointed out the yield of grain apparently is more affected by a deficiency of magnesium than is the stover.

TABLE 2.—*Mean and relative yields of crops grown with fertilizer and added magnesium sulphate and lime, 1929 to 1934*

Crop	Years in which grown	Yield per acre (fertilizer only)	Relative yield [1] with fertilizer plus—		
			Magnesium sulphate	Magnesium sulphate and lime	Lime
		Bushels			
Corn, field (grain)	1929 to 1934	42.5	95.0	100.7	99.2
		Pounds			
Corn, field (stover)	1929 to 1934	[2] 2,147	99.7	107.8	112.2
		Bushels			
Potatoes	1929 to 1931	204.3	105.7	106.3	97.0
Onions (from sets)	1929, 1930	109.2	87.0	127.0	128.0
Onions (from seed)	1931	70.3	89.0	111.0	118.0
		Pounds			
Timothy	1930, 1931	[2] 3,605	99.5	95.5	106.5
Clover (alsike)	1930 to 1932	[2] 3,683	101.0	101.3	100.0
Soybeans (forage)	1931, 1932	[2] 4,480	105.0	107.0	104.0
Buckwheat (grain and straw)	1932, 1933	[2] 2,020	128.5	122.5	101.0
Oats (grain and straw)	1932, 1933	[2] 4,262	102.5	95.0	97.0
Barley (grain and straw)	1933, 1934	[2] 3,288	90.5	101.5	100.0
Sudan grass	1933, 1934	[2] 3,750	97.0	91.0	103.0
Millet (Japanese)	1933, 1934	[2] 6,298	100.0	93.0	88.0
Rutabagas (early planting)	1933, 1934	37,608	103.0	108.5	102.0
Rutabagas (late planting)	1933	9,762	110.0	154.0	127.0
Corn, sweet (ears)	1934	[2] 1,803	95.0	98.0	107.0
Corn, sweet (stover)	1934	[2] 2,914	100.0	103.0	122.0
Mangels (roots)	1934	85,507	118.0	114.0	110.0
Turnips (White Egg)	1934	17,760	113.0	89.0	91.0
Spinach	1934	[2] [3] 402	138.0	208.0	208.0
Peppers (fruit)	1934	10,317	96.0	108.0	112.0
Peppers (plants)	1934	[2] 655	93.0	100.0	103.0

[1] Yield with fertilizer only taken as 100.

[2] Dried in steam-heated oven to approximately 4 percent water. Work done in feed-control laboratory under supervision of P. H. Smith.

[3] The comparatively low figure for the yield of spinach is due largely to the fact that the plants were more widely spaced than is usual in practice, and probably in part to a lower level of fertility than is common in vegetable gardening. However, it should be noted that yield figures are for dry matter rather than green weight.

[6] Jones, J. P. (See footnote 2.)

A gravelly ridge running diagonally across the field is particularly effective in reducing yields of the magnesium-treated sections of plots 3 and 4 in dry seasons. This condition, together with a more favorable moisture relation of the checks, particularly of plot 3, is favorable to the checks in dry seasons. The variation in the yields from the different sections of the plots is shown by table 3. If plots 1, 2, and 4 are taken as more representative of uniform conditions, it will be seen that, except for the stover, the magnesium-treated sections were relatively better (e. g., 46.2 bushels *v.* 41.7 bushels) than the checks without lime. With lime this is true of plot 2 only. In the wet year of 1931 the yield of the magnesium-treated section of plot 1 exceeded that of the check by 27.9 percent for both grain and stover.

The effect of season on the absorption of available magnesium is well shown by the data on amount of chlorosis given in table 4. Here it will be noted that the highest percentage of chlorotic plants occurred in the wet year 1931. By comparing table 4 with the precipitation data it will be seen that there is almost perfect agreement between precipitation and extent of chlorosis in corn.

TABLE 3.—*Mean yield of corn, grain, and stover, as affected by additions of magnesium sulphate and lime, by plot sections, 1929–34*

Crop and plot	Yield on plots treated with fertilizer plus—			
	Nothing	Magnesium sulphate	Magnesium sulphate and lime	Lime
Corn (grain):	*Bushels*	*Bushels*	*Bushels*	*Bushels*
Plot 1	41.1	44.0	44.7	50.0
Plot 2	41.7	46.2	45.9	30.6
Plot 3	51.2	29.8	37.3	42.6
Plot 4	36.1	41.7	43.3	45.6
Corn (stover):	*Pounds*	*Pounds*	*Pounds*	*Pounds*
Plot 1	2,101	2,501	2,617	2,744
Plot 2	2,166	2,156	2,443	2,090
Plot 3	2,589	2,135	2,313	2,526
Plot 4	2,032	2,205	2,368	2,625

TABLE 4.—*Percentage of normal and chlorotic corn plants as influenced by addition of magnesium sulphate and lime, 1929–34*

Year	Treatment in addition to fertilizer	Plants that were—			Year	Treatment in addition to fertilizer	Plants that were—		
		Normal	Chlorotic				Normal	Chlorotic	
			Slightly	Strongly				Slightly	Strongly
		Pct.	*Pct.*	*Pct.*			*Pct.*	*Pct.*	*Pct.*
1929	None	39	18	43	1932	None	16	45	39
	Magnesium sulphate	87	9	4		Magnesium sulphate	100	0	0
	Magnesium sulphate and lime	85	9	6		Magnesium sulphate and lime	100	0	0
	Lime	84	9	7		Lime	79	19	2
1930	None	35	54	11	1933	None	9	37	54
	Magnesium sulphate	98	2	0		Magnesium sulphate	100	0	0
	Magnesium sulphate and lime	96	4	0		Magnesium sulphate and lime	98	2	0
	Lime	79	20	1		Lime	70	25	5
1931	None	5	40	55	1934	None	20	46	29
	Magnesium sulphate	85	14	1		Magnesium sulphate	100	0	0
	Magnesium sulphate and lime	78	20	2		Magnesium sulphate and lime	100	0	0
	Lime	39	52	9		Lime	95	4	1

Of all crops grown, buckwheat and spinach were most affected by a deficiency of magnesium, but as there are only 1 year's results for spinach, they must be considered as indicative only.[7] The yield of buckwheat was not only considerably increased by magnesium, but the physiological symptoms also were marked. This crop appears to be the most sensitive to magnesium deficiency of all those studied in this experiment. It will be noted that the beneficial effects of magnesium are enhanced by the addition of lime.

PHYSIOLOGICAL SYMPTOMS

One of the principal objectives of this work was the determination of the plant symptoms associated with magnesium deficiency. Con-

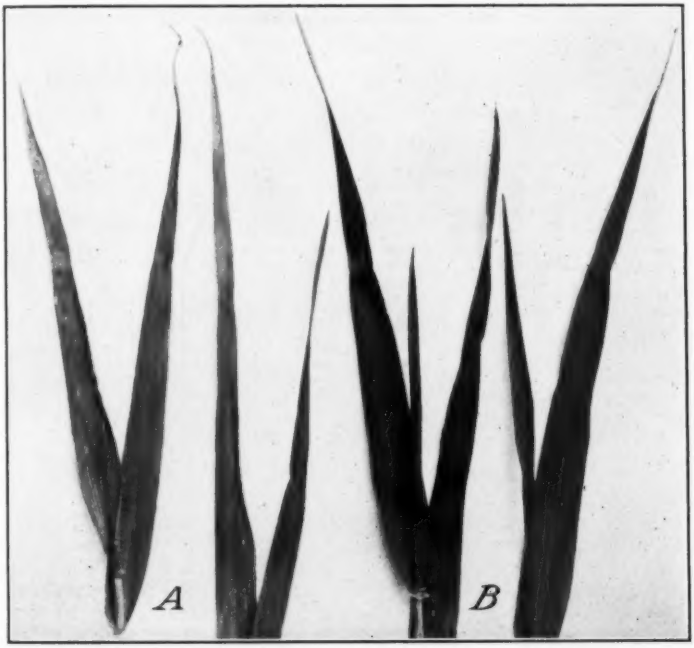

FIGURE 1.—Barley leaves: *A*, Mildly chlorotic, striped type, from magnesium-deficient soil; *B*, normal, from soil treated with magnesium sulphate.

siderable difference in the effect of the deficiency was noted among the crops grown. The more sensitive species developed symptoms which varied from a mild chlorosis to extreme necrosis of the leaf tissue.

Jones, in a previous report[8] on this work, accurately described the symptoms of this physiological disease as it affects corn, and Garner and others[9] have described its effects on tobacco. Nothing needs to be added to Jones' description of the symptoms on corn

[7] Pot experiments in the greenhouse appeared to corroborate the field observations on spinach.

[8] JONES, J. P. See footnote 2.

[9] GARNER, W. W.; MCMURTREY, J. E.; BACON, C. W., and MOSS, E. G. SAND DROWN, A CHLOROSIS OF TOBACCO DUE TO MAGNESIUM DEFICIENCY, AND THE RELATION OF SULPHATES AND CHLORIDS OF POTASSIUM TO THE DISEASE. Jour. Agr. Research 23:27-40, illus. 1923.

except to state that incipient chlorosis sometimes appeared first on the margin and tip of the leaves instead of in the intervascular tissue. On other soils having a severer deficiency of magnesium it has been observed that corn leaves crinkle and droop considerably in advanced stages of the disease.

The pattern of chlorosis developed by other plants followed rather closely the type of venation of the leaves. Leaves having parallel veins, such as certain small grains and grasses, developed the same type of chlorosis as corn, but of a mild type (fig. 1). Oats showed the symptoms in an early stage of growth, but they later disappeared. It should be stated that some parallel-veined plants have leaves that normally are more or less striped, or else the striping is due to some deficiency other than magnesium. Such was the case with Japanese millet. The effect of magnesium deficiency on the different plants used in the experiment is shown in table 5.

TABLE 5.—*Plant symptoms produced by a moderate magnesium deficiency in the soil*

Plant	Chlorosis			Remarks	Plants	Chlorosis			Remarks
	None	Mild	Strong			None	Mild	Strong	
Corn (field)	---	X	X	Striped, necrotic.	Barley	---	X	---	Striped.
Corn (sweet)	---	X	X	Do.	Sudan grass	---	X	---	Do.
Potato	X	X	---		Millet (Japanese)	X	---	---	
Onion	X	---	---		Rutabaga	---	X	X	Mottled.
Timothy	X	---	---		Mangel	---	X	---	Do.
Clover (alsike)	X	X	---	Marginal, mottled.	Turnip (White Egg)	---	X	X	Do.
Clover (red) [1]	X	---	---		Spinach	---	X	X	Sunscald necrosis.
Alfalfa [1]	X	---	---		Pepper	---	X	---	Mottled.
Soybean	---	X	---		Tobacco	---	X	X	Do.
Buckwheat	---	X	X	Mottled, necrotic.					
Oat	---	X	---	When young, only.					

[1] Pot experiment.

Susceptible plants with leaves of netted venation as a rule developed a mottled pattern similar to the well-known appearance of tobacco leaves affected by "sand drown." Buckwheat and turnips (and tobacco in the earlier experiment on this soil) were the outstanding plants which showed this type of chlorosis (figs. 2 and 3). With these plants, also, incipient chlorosis often appeared in the leaf margin instead of in the intervascular tissue. In advanced stages of the disease cupping or curling of the leaf margin was common, the tissue turned yellow or brown, and the leaves dropped from the plant. A necrosis of intervascular tissue similar to sunscald often occurred, particularly in leaves exposed to full action of the sun's rays.

Spinach was affected differently. The typical chlorosis shown by other plants did not appear, but instead marked necrotic areas developed in the intervascular tissue. These areas were whitish and of a papery texture, and similar to sunscalded areas (fig. 4). They appeared within a very short time after conditions were right. It is thought that lesions of this kind might be expected in the mesophyllic tissue of a leaf of a rapidly growing plant like spinach if the tissue were deficient in some essential ingredient. Apparently this tissue in its condition of rapid growth and tenderness skipped the usual

chlorotic stage or passed through it so rapidly that it was not observed. The observations of only 1 year are available on this crop and conclusions can, therefore, be only tentative.

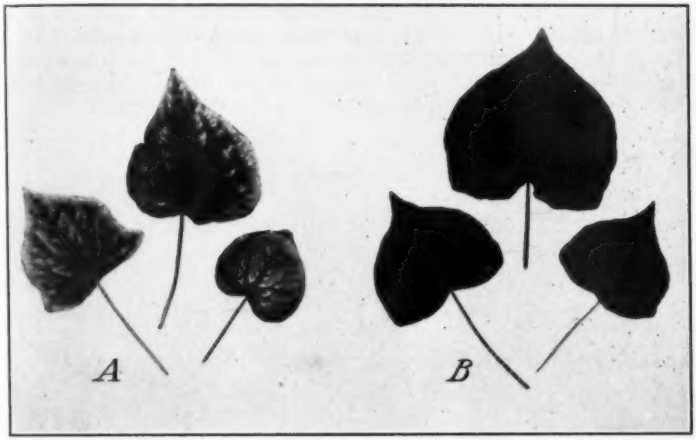

FIGURE 2.—Buckwheat leaves: *A*, Strongly chlorotic and necrotic, mottled type of chlorosis, from magnesium-deficient soil; *B*, normal, from soil treated with magnesium sulphate.

A characteristic symptom of magnesium deficiency observed in these experiments is that the chlorosis appeared first on the older

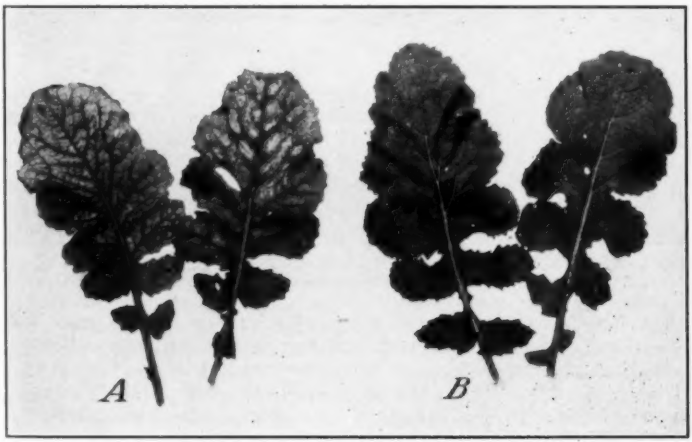

FIGURE 3.—Turnip leaves: *A*, Strongly chlorotic and necrotic, mottled type of chlorosis, from magnesium-deficient soil; *B*, normal, from soil treated with magnesium sulphate.

leaves, regardless of the type of plant. This characteristic should serve to distinguish the chlorosis due to magnesium deficiency from that due to some other causes.

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EFFECT OF MAGNESIUM DEFICIENCY ON CHEMICAL COMPOSITION OF PLANTS

The effect of magnesium deficiency in this soil on the mineral constituents of different parts of the corn plant has been reported by Jones.[10] His data showed that the content of magnesium in the plant corresponded to the application of magnesium sulphate to the soil. Work along this line has been continued in the present studies. In table 6 are given analytical results for the years 1930, 1931, and 1933. The rainfall during the growing season of 1931 was unusually

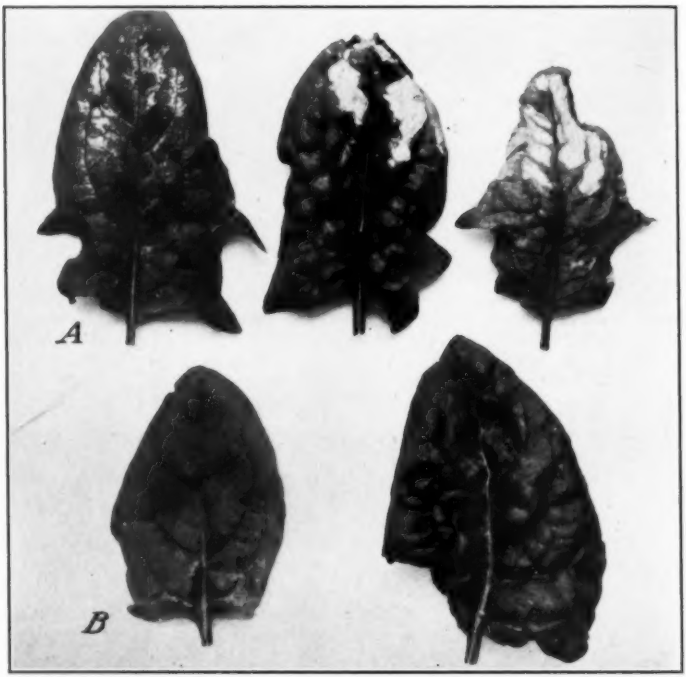

FIGURE 4.—Spinach leaves: *A*, Necrotic, from magnesium-deficient soil; *B*, normal, from soil treated with magnesium sulphate.

high, 6.4 inches above normal, while that of the other 2 years was a little below normal. This difference in precipitation is reflected in the magnesium content of the corn stover, which was lowest in the wet year of 1931. The data as a whole show that the magnesium content of the crop was enhanced by applications of magnesium sulphate to the soil. This increase was greatest in those crops, such as buckwheat, that showed the greatest response to magnesium in yield and symptoms.

[10] JONES, J. P. (See footnote 2.)

TABLE 6.—*Percentage magnesium oxide and calcium oxide in dry matter of several crops grown with fertilizer only and with fertilizer and added magnesium sulphate and limestone* [1]

Year and crop	Analysis of plants from plots treated with fertilizer plus—							
	Nothing		Magnesium sulphate		Magnesium sulphate and lime		Lime	
	MgO	CaO	MgO	CaO	MgO	CaO	MgO	CaO
1930: [2]	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Corn stover	0.183	0.603	0.338	0.580	0.315	0.605	0.228	0.625
1931: [2]								
Corn stover	.143	.605	.308	.523	.268	.585	.208	.730
1933: [3]								
Corn and cob	.151	.139	.247	.138	.187	.127	.187	.145
Corn stover	.229	.634	.395	.541	.372	.568	.299	.692
Oats (grain and straw)	.518	.680	.604	.614	.679	.690	.529	.715
Barley (grain and straw)	.427	.733	.595	.719	.657	.668	.436	.805
Sudan grass	.709	1.150	.699	1.200	.537	1.129	.511	1.134
Millet	.608	1.311	.769	.990	.694	1.528	.618	1.330
Buckwheat (grain and straw)	.442	3.360	.728	2.468	.592	3.075	.475	4.064
Rutabagas (roots)	.308	.794	.245	.979	.205	.776	.181	.961
Rutabagas (tops)	.289	3.409	.466	3.071	.394	3.935	.331	4.081

[1] Chemical work was done in the fertilizer control laboratory under direction of H. D. Haskins.
[2] Mean of analyses of samples from 4 replicated plots, 1930 and 1931.
[3] In 1933 analyses were of composited samples from 4 replicates.

GENERAL DISCUSSION

Observations and studies recently made of other magnesium-deficient soils in the Connecticut Valley indicate that the soil on which these experiments were conducted is only moderately deficient in magnesium. Many more extreme cases have been observed, and these were on soils containing somewhat less of the finer separates and often much more gravel. Magnesium deficiency on such soils has been found to be associated with moderate to strong acidity, and no doubt much of the trouble with crop growth was due to strong acidity or calcium deficiency, or both.

The unlimed half (secs. C and D) of the field used for these experiments has a reaction of pH 5.6 and the limed half pH 6.4. Some Connecticut Valley soils showing extreme magnesium deficiency have tested about pH 4.0. Some of these extreme cases have shown also a much greater magnesium deficiency by the rapid colorimetric field tests than the soil of the field used in these experiments. The surface soil of this field was found to contain from 8.7 to 20.3 parts per million of magnesium in the untreated section, by extraction with potassium chloride,[11] and these figures agree fairly closely with the estimates by the rapid semiqualitative methods. The untreated surface soil contained 0.747 percent total magnesium. It appears that a soil should contain from 30 to 40 parts per million of easily replaceable magnesium, or 60 to 80 pounds per acre, to avoid magnesium deficiency.

[11] HADDOCK, J. L. STUDIES OF METHODS FOR DETERMINATION OF MAGNESIUM DEFICIENCY IN SOILS. 1932. (Unpublished thesis.)

SUMMARY

The crops grown differed to a marked degree in their response to a deficiency of magnesium in the soil. Buckwheat and spinach were most affected, and turnips, mangels, corn, and tobacco considerably so. The small grains, grasses, clovers, and potatoes were only slightly affected, and other plants not at all. Plants sensitive to magnesium deficiency developed characteristic physiological symptoms which have value in diagnosis. Chlorosis of the older leaves developed in the intervascular tissue. In the leaves of plants with parallel veins this produced a striped appearance, while in the leaves having netted venation, a mottled pattern was produced. In severe cases of chlorosis the margin or the entire leaf turned brown, and in some cases the leaf dropped from the plant.

The addition of magnesium sulphate to the soil increased the percentage of magnesium in the plant or portions of it. The increase was greatest in those crops whose yields and appearance were most affected by the deficiency of magnesium. The content of magnesium in the plant was affected also by the amount of precipitation during the growing season, being less in seasons of heavy rainfall.

THE SUSCEPTIBILITY OF FLOWER BUDS OF THE MONTMORENCY CHERRY TO INJURY FROM LOW TEMPERATURE [1]

By V. R. GARDNER

Director, Michigan Agricultural Experiment Station

INTRODUCTION

Injury to flower buds or developing flowers from low temperatures has long been recognized as in some degree a limiting factor in sour-cherry production. Nevertheless, most varieties of sour cherry (*Prunus cerasus L.*) are regarded as comparatively hardy, their flower buds being as resistant to cold in midwinter as those of the apple, though in the preblossoming stage of early spring they become more tender than those of the peach. Goff [2] reported that a comparatively large percentage of the flower buds of most varieties survived a minimum temperature of −27.5° F. at Madison, Wis., in 1899, though somewhat more serious injury was recorded following the milder winter (−23° minimum) of 1896–97, which had been preceded by a rather dry summer. Temperatures ranging from −22° to −37° in February 1934, at various points in northern Michigan where the Montmorency is extensively grown, killed from 5 to 20 percent of the buds (as determined by random sampling), hardly enough greatly to reduce the size of the following crop. On the other hand, data collected by the Michigan Agricultural Experiment Station during recent years in connection with its study of bud variation indicate that the number of flower buds killed at comparatively low temperatures is sometimes smaller than at other times when the temperature is somewhat higher, and that there is much variation between trees in the same orchard in susceptibility to injury of this kind. Records bearing on certain aspects of this question are presented in this paper.

KILLING OF DORMANT FLOWER BUDS BY LOW TEMPERATURES

Besides winter-killing records on certain individual Montmorency trees, selected because of apparent marked susceptiblity or resistance of the flower buds to winter cold, counts were made on large random samples of buds from each of 149 trees in a block on the grounds of the Graham Horticultural Experiment Station at Grand Rapids, Mich., following the winters of 1932–33 and 1933–34, and in the so-called "Corporation" orchard of 190 trees near South Haven, Mich., for the same years. Minimum temperatures of −10° F. and −16° were recorded on February 9 of both years at Grand Rapids and −10° and −17° on the same dates at South Haven.

Killing of individual flowers in the buds ranged from 0 to 5 percent in the winter of 1932–33 at Grand Rapids and from 2 to 37 percent in the winter of 1933–34. Averages for the 2 years were 0.7 and 11.5

[1] Received for publication Nov. 20, 1934; issued May 1935. Journal article no. 196 (N. S.) from the Michigan Agricultural Experiment Station.

[2] GOFF, E. S. THE DEGREE OF COLD ENDURABLE BY FLOWER-BUDS OF THE PLUM AND CHERRY. Wis. Agr. Expt. Sta. Ann. Rept. 14: 309-313, illus., 1897.

percent. At South Haven killing of individual flowers in the bud ranged from 0 to 22 percent in the winter of 1932–33 and from 0 to 21 percent in the winter of 1933–34. Averages for the 2 years were 5.7 and 5.6 percent. The period covered by these figures is too short to establish them as an accurate measure of the extent to which the dormant flower buds of this variety are winter-killed, but when they are considered in connection with observations extending over many years the conclusion seems warranted that bud killing of this type is not an important limiting factor in the production of Montmorency cherries in Michigan. Doubtless, killing of individual flowers in excess of 20 percent is likely to lead to some reduction in yield, though the higher percentages of blossoms that set fruit under such conditions usually compensate in part for the reduction in flower number. A com-

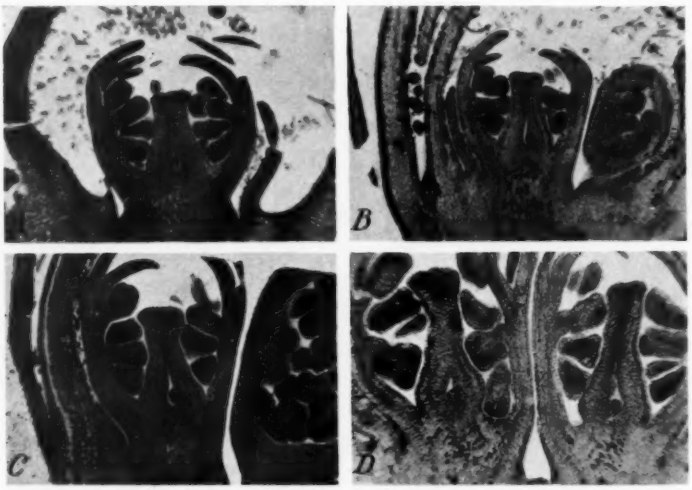

FIGURE 1.—Photomicrographs showing representative flower-bud development in a sport of the Montmorency cherry whose buds are especially tender to low winter and spring temperatures, compared with normal buds: *A* and *C*, Buds of Selection 159, which is tender to cold, collected November 2, 1932, and March 28, 1933; *B* and *D*, buds from adjacent normal Montmorency trees collected the same dates. × 33.

parison of injury in individual trees for 2 years is possible only from the records of the Corporation orchard. Only a few trees whose buds were injured rather severely one winter showed a high degree of injury the next winter. However, this is not surprising in view of the relatively small differences between these trees.

Buds from a number of trees in both the Graham Station and Corporation orchards which showed some of the most and some of the least winter-killing were collected in late fall and again in early spring for sectioning, to determine whether such differences as were found in resistance to low winter temperatures might be correlated with differences in state of advancement. The flower buds themselves, their rudimentary pistils, and their other flower parts varied more or less in size from tree to tree when collected, say, November 1 or March 15, but the degree of differentiation attained at any particular date in any 1 year varied very little between trees in a single locality.

Furthermore, the slight variations above or below the average in size and in degree of differentiation were about equally distributed among trees with the more hardy and those with the less hardy buds. A study of the buds of a Montmorency tree in an orchard near Sodus, Mich., planted in 1904 and always semibarren, furnishes additional evidence on this latter point. This tree, to be regarded as a bud sport,[3] forms an abundance of flower buds that at the close of the growing season cannot be distinguished from those of surrounding, normally productive trees. Nor can the buds which survive the winter be distinguished in early spring from those on adjacent trees.

However, about two-thirds of the buds are regularly winter-killed. Their tenderness is due to or associated with some physiological condition rather than with any peculiarity of structure. This is well brought out in figures 1 and 2, which show the flower parts of average

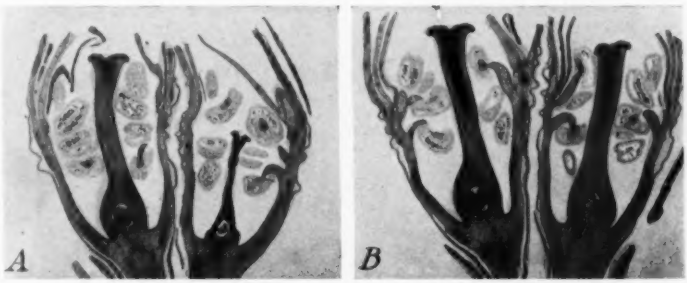

FIGURE 2.—Representative flower buds of a sport of the Montmorency cherry whose buds are especially tender to low winter and spring temperatures, compared with normal buds: *A*, Buds of Selection 159, which is tender to cold and one of whose flowers had been killed by frost 3 days previous to collection on April 29, 1933; *B*, buds of an adjacent Montmorency tree more resistant to low temperatures, collected the same date. × 7.

flower buds from this winter-tender tree, along with those from adjacent normal trees, collected at intervals.

DELAYED WINTER-KILLING OF FLOWER BUDS BY LOW TEMPERATURES

Montmorency buds in which all of the individual flowers have been killed during the dormant season rarely enlarge in the spring, and their bud scales do not separate even at the tip. As the season advances they dry out, an abscission layer forms at their bases, and by the middle or end of the blossoming season most of them have fallen off. Buds in which some of the individual flower buds have been killed but in which one or more have survived enlarge and open very much like those in which none of the individual flowers has been harmed. Many buds enlarge to several times their winter size, reflex their outer scales, and expand their inner scales without, however, protruding any blossoms. The exposed outer surfaces of the inner bud scales acquire a purplish pink color. Finally, at about the full-bloom stage these buds that several weeks earlier gave promise

[3] The term "bud sport" is used in this article to refer to a whole-tree or limb variant that has been under observation for a number of years so that the permanence of its deviation from type in the orchard or in the tree is established. In most of the instances cited the variant and the accompanying parent or normal form have been propagated vegetatively, but in only a few instances have the daughter trees been under observation long enough to permit a comparison of their behavior with that of the parent forms.

of producing a full crop of flowers, fall off. Examination shows that the bud that behaves in this way survived the winter and resumed growth and differentiation in the spring. As growth is resumed, however, the developing flower buds become relatively susceptible

FIGURE 3.—*A*, A spur showing 2 flower buds (*aa*) killed during the dormant season and 2 in each of which 2 individual flowers were uninjured; *B*, *C*, 2 twigs showing flower buds that had all or part of their individual flowers killed by the late type of winter-killing: *D*, 1 flower bud (*a*) on this shoot had all its individual flowers killed while dormant, 2 buds (*b*) suffered no winter-killing of either the dormant season or late type, and the others had all or part of their individual flowers killed by the late type of winter-killing. Photo taken May 15, 1934.

to injury from low temperatures, and observations indicate that this is a far more critical period than the dormant season. The data indicate further that there are wide variations between different trees in the same orchard growing under the same conditions, and also between different limbs of the same tree, in the susceptibility of their

flower buds to killing at this stage. The difference between this late form of winter-killing of flower buds and that which occurs while the buds are dormant is shown in figure 3, and the difference in stage of development of the individual flowers and flower parts at the time the injuries occur is shown in figure 4.

Sharp demarcation of dormant-season killing from killing associated with early growth resumption cannot be made. This latter, in turn, merges into still later killings of buds near or at the blossoming stage. However, the failure of the early killed buds to swell in the one case

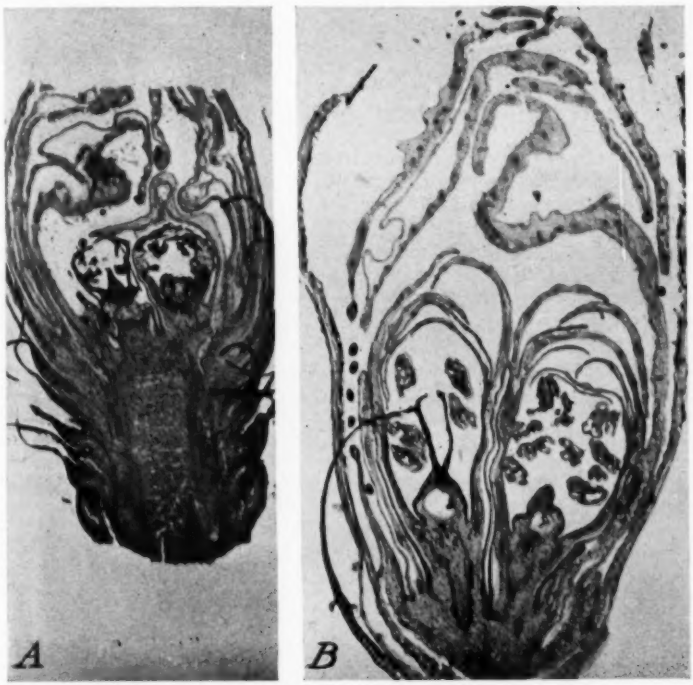

FIGURE 4.—Sections of flower buds of the Montmorency cherry showing killing from midwinter freezing (*A*) and killing of the late winter type (*B*). Both sections are of buds collected May 15 when the trees were in full bloom. × 13.

and of the individual flower buds to protrude beyond the separating bud scales in the other fairly accurately delimits what is here described as delayed winter-killing. Assignment of this type of injury to winter or to spring is largely a matter of judgment, but it occurs at a stage when advancement from dormancy is so slight that it may be regarded as a type of winter-killing. So far as the writer is aware, this type of winter-killing has not been described or recognized in the literature dealing with the sour cherry.

Extensive quantitative data are not available to show the amount of this form of bud killing in different sections or in different years. That it may sometimes be serious, however, is indicated by the fact that in a random sample of flower buds from one large Montmorency

tree in an orchard near Traverse City, Mich., examined May 15, 1934, all of the individual flowers were dead in 71 percent of the buds and about 70 percent of the blossoms in the remaining 29 percent; that is, the total blossom killing amounted to over 90 percent. Many other trees in the same orchard suffered serious injury of the same type, though none quite so heavily. Observations in many Montmorency cherry orchards of Michigan during the past 10 years lead to the opinion that in general between 5 and 10 times as many flower buds are killed while in this early post-dormant stage as are killed by much lower temperatures in the dormant stage. Unquestionably delayed winter-killing is a factor of considerable importance in limiting yield in the Montmorency cherry orchards of Michigan, though it is less serious than spring frost injury, which comes still later.

KILLING OF FLOWER BUDS BY SPRING FROSTS

Every cherry grower recognizes the danger of the serious reduction or perhaps entire loss of his crop from the killing of fully opened blossoms or of unopened blossom buds by spring frosts. Indeed, this is generally considered the greatest hazard in sour cherry production, even more of a hazard than it is with most other deciduous fruits because of the apparent greater susceptibility of the flowers to frost injury. Some measure of its importance may be obtained from records collected for the 149 Montmorency trees at the Graham Station for the years 1932–34. In the spring of 1932 the percentage of blossoms or blossom buds killed by spring frost on different trees ranged from 32 to 99, with an average of 77; in the spring of 1933 the range was from 20 to 90, with an average of 60; and in the spring of 1934 the range was from 1 to 95, with an average of 25. In the Corporation orchard killing by spring frosts on the 190 trees ranged from 4 to 100 percent in 1931, with an average of 56; from 25 to 97 percent in 1933, with an average of 73. There was no frost injury in this orchard in 1932 or 1934. In some orchards the loss would be distinctly smaller, in others much greater.

Records for individual trees in these two and in a number of other orchards show clearly that, though some trees present considerable variation in the relative amount of frost injury from year to year, many others are remarkably consistent in the reaction to cold of their open flowers or unopened flower buds. This is well brought out in tables 1 and 2.

TABLE 1.—*Percentages of blossoms killed by frost in the Graham Station and the Corporation orchards, 1931–34*

Orchard and trees	Percentage of blossoms killed in—			
	1931	1932	1933	1934
Graham Station:				
All trees		77	60	25
25 trees most injured in 1932		94	64	25
25 trees most injured in 1933		82	80	19
25 trees most injured in 1934		80	60	68
25 trees least injured in 1932		54	49	16
25 trees least injured in 1933		63	40	21
25 trees least injured in 1934		76	57	2
Corporation:				
All trees	55.8	0	73.0	0
25 trees most injured in 1931	98.0	0	85.0	0
25 trees most injured in 1933	81.0	0	92.7	0
25 trees least injured in 1931	10.9	0	61.0	0
25 trees least injured in 1933	32.0	0	46.0	0

TABLE 2.—*Records of spring frost injury to selected trees in the Graham Station and the Corporation orchards, 1931–34*

Orchard	Tree no.	Percentage of blossoms killed in—			
		1931	1932	1933	1934
Graham Station	5B	(1)	49	41	4
	5H	(1)	55	45	1
	3J	(1)	63	38	3
	2E	(1)	90	58	92
	4E	(1)	93	55	94
	9E	(1)	94	70	93
Corporation	21	8	0	39	0
	47	8	0	37	0
	137	14	0	25	0
	59	100	0	94	0
	125	95	0	97	0
	144	95	0	95	0

[1] Undetermined.

In view of the fact that as cherries approach the blossoming stage more or less unevenness in degree of development of the flower buds

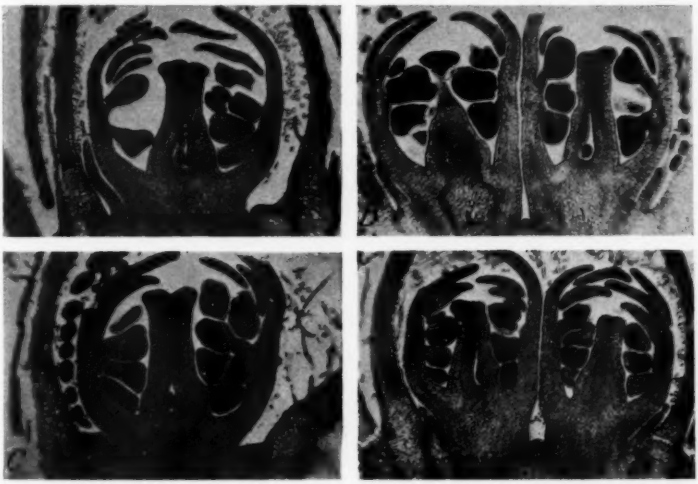

FIGURE 5.—*A* and *B*, photomicrographs showing development of representative flower buds of selection 516, a tree normally resistant to injury from midwinter cold and from spring frost, collected November 9, 1932, and March 29, 1933, respectively; *D* and *C* are photomicrographs showing development of representative flower buds of selection 517, a bud sport in tree no. 516, the buds of which are relatively susceptible to injury from midwinter cold and spring frost, collected November 9, 1932, and March 29, 1933, respectively. Note that the buds of selection 517 are practically indistinguishable from those of selection 516. × 33.

is always in evidence, the question naturally arises whether the more advanced or the less advanced flowers suffer most from a damaging frost. The answer is that, in general, when flower buds are one-quarter to one-half the size they attain just before they open they appear to be slightly but distinctly more sensitive to frost injury than when they are fully developed and ready to open or when the flower is partly open or fully expanded, though this may be associated with the fact that the frosts occurring during the earlier stages of development are usually more severe than those occurring a few days later.

Large numbers of field records, however, warrant the definite statement that the differences in susceptibility from tree to tree are so great and the differences in advancement so small, that direct connection between them seems improbable.

Examinations were made of sections of random samples of large numbers of flower buds from a considerable number of individual

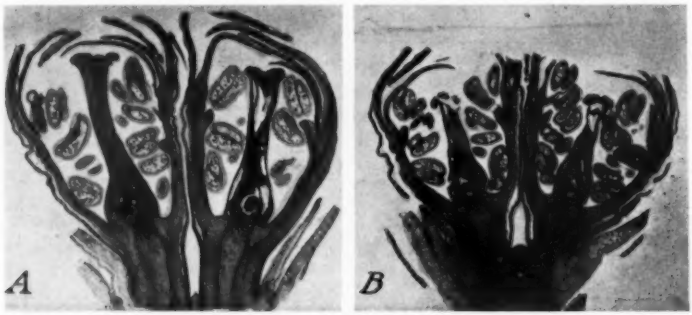

FIGURE 6.—Flower bud of the relatively frost-resistant normal form (selection 516) of the Montmorency cherry (*A*) and of a bud sport (selection 517) of the same tree (*B*) the buds of which are relatively tender to frost. Material collected for sectioning April 29, 1933, 3 days after the frost occurred; 1 injured pistil in *A*. Note that there is relatively little difference in stage of development between the frost-resistant and frost-susceptible buds though there is some difference in sizes of flower parts. × 10.

Montmorency trees and of their limb sports, collected at various periods (e. g., June 30, July 15, Aug. 15, Nov. 1, late March, mid-April, late April). The results showed that in the relatively late blossoming trees or limb sports and in those that blossom rather early, in those whose flower buds are relatively susceptible and in those whose flower buds are very resistant to spring frost injury

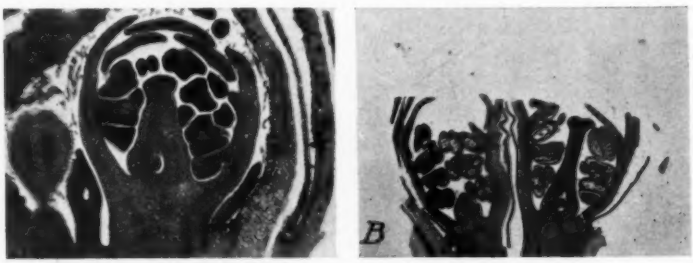

FIGURE 7.—Representative flower buds of selection 365, a frost-tender but late-blossoming sport of the Montmorency cherry. Comparison of the March 28 collection *A* (× 33) with *B* and *C* in figure 5 show that the buds of this sport had reached a normal stage of development in late winter. Comparison of the April 29 collection *B* (× 10) with *A* and *B* in figure 6 indicates a slower development in early spring.

(1) the flower buds are differentiated at practically the same time of the year, (2) the buds attain essentially the same stage of differentiation at the beginning of the dormant season, (3) bud growth is resumed at practically the same time in late winter or early spring, (4) initial growth rate in the spring is essentially the same, but (5) as the growing season advances differences in rate of development become increasingly pronounced. These statements are supported by the photomicrographs shown in figures 5, 6, and 7, selected as

fairly representative of many thousands of buds that were examined. The evidence, therefore, indicates clearly that the major differences in susceptibility to spring frost are of a nature not revealed by anatomical study. It also indicates that cultural methods intended to hasten or delay flower-bud differentiation or advancement, do not afford a very promising approach to the solution of the frost-injury problem in the Montmorency cherry although in Wisconsin some relationship between early differentiation and advanced fall development on the one hand and susceptibility to low winter temperatures on the other has been reported.[4]

CORRELATION BETWEEN THE DIFFERENT TYPES OF INJURY TO FLOWER BUDS CAUSED BY LOW TEMPERATURES

The question arises whether a whole tree bud sport or a limb sport whose flower buds are markedly resistant or markedly susceptible to one form of injury is likewise markedly hardy or markedly tender to another form. The data collected indicate that a sport whose flower buds are, say, especially susceptible to winter-killing while in the dormant state are neither more nor less likely to be susceptible to late winter-killing or to spring frost injury. For instance, on selection 365, a whole-tree variant in the Corporation orchard, the flower buds were killed to the extent of 100 and 93 percent in late April of 1931 and 1933, but none of its flower buds were killed by mid-winter freezing in 1932–33 and only 2.5 percent were killed during the much severer winter of 1933–34. At no time during the 1930–34 period did the flower buds on this tree show an appreciable amount of the late form of winter-killing. Selection 420, a whole-tree variant in the Titus orchard at Traverse City, had 17 percent of its individual flower buds destroyed by a minimum temperature of −35° F. on February 9, 1934, whereas none of a considerable number of nearby trees showed a loss of more than 10 percent. On the other hand, in the spring of 1932, when these same surrounding trees had from 20 to 90 percent of their flower buds destroyed by the late type of winter-killing and by spring frost combined, selection 420 had less than 5 percent of its blossoms destroyed by these 2 types of injury together. Again, in the spring of 1934 when the killing of opened and unopened flower buds on surrounding trees ranged from 10 to 15 percent, not a single frost-injured blossom could be found on selection 420. The observation of the foreman of this orchard that for 7 consecutive years this particular tree had not failed to bear a heavy crop, while frost had levied a tax more or less frequently on surrounding trees, and that in 1928 it was 1 of only 2 trees that bore a crop when a late April freeze destroyed the crop on all other trees in the orchard, is further evidence of an exceptional degree of hardiness of its flower buds to late winter-killing and to spring frosts. Tree G in row 11 at the Graham Station orchard had none of its individual dormant flower buds destroyed by low temperatures in the winter of 1932–33 and only 9 percent in the much severer winter of 1933–34. These compare with averages of 0.7 and 11.9 for the entire orchard. Loss of individual blossoms and blossom buds from late spring frosts amounted to 79, 65, and 35 percent in 1932, 1933, and 1934, respectively, with averages for the entire orchard

[4] ROBERTS, R. H. WINTER INJURY TO CHERRY BLOSSOM BUDS. Amer. Soc. Hort. Sci. Proc. 14 : 105-110, illus. 1917.

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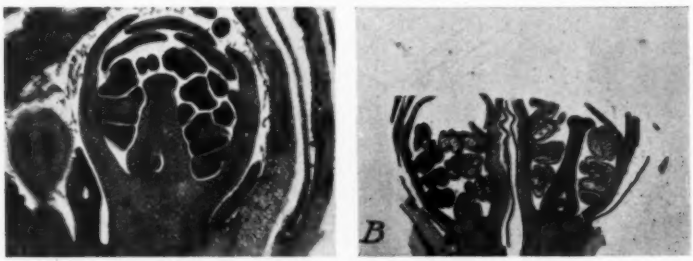

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of 77, 60, and 25 percent. Obviously, the flower buds of this tree are not especially susceptible to injury from low temperatures while in the midwinter dormant state or during the short preblossoming and blossoming stages when spring frosts are likely to cause trouble. Yet in 1934 out of a random sample of 4,074 flower buds, from this tree containing an estimated 12,000 individual flowers, only 2,587 (or 22 percent) of the flowers survived the late winter type of killing. This was a far higher percentage of late winter-killing of flower buds than was found on any other tree in the orchard and indicates an especially marked susceptibilitv to this particular type of injury.

DISCUSSION

The data here presented on intravarietal variations in hardiness of flower buds at different stages in their development explain in part some of the irregularities in production that have been observed in Montmorency cherry orchards. A tree that is relatively productive one year and unproductive the next while the reverse is true of an adjacent tree may simply be especially sensitive or resistant to some one of the several types of injury from low temperature. The fact that the Montmorency variety, as it is ordinarily propagated and grown, evidently includes not only forms whose flower buds are relatively susceptible and relatively resistant to low temperatures at each of three fairly distinct stages but various combinations of resistance in these several stages, both indicates what to expect in the way of intravariety diversity and deterioration from a careful field survey of the losses from low temperatures and suggests that the approach to the practical solution of the problem lies in the isolation and propagation of strains whose flower buds are relatively cold-resistant at all stages of their development.

SUMMARY

Developing flower buds of the Montmorency cherry are killed by low temperatures at three different stages—while dormant, soon after growth is resumed within the bud in the spring, and in the preblossoming or blossoming stage.

Susceptibility to injury at any of these stages is not closely correlated with the degree of differentiation or development that has been attained.

The Montmorency variety includes a number of forms which show great variation in their susceptibility to low temperatures at these several stages.

Susceptibility to injury from low temperatures at one of these stages is not correlated with susceptibility at another stage.

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